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Nearshore Fish Assemblage Patterns with Respect to Landscape-Scale Habitats in Central California

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NEARSHORE FISH ASSEMBLAGE PATTERNS WITH RESPECT TO LANDSCAPE-SCALE HABITATS IN CENTRAL CALIFONIA

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ABSTRACT

NEARSHORE FISH ASSEMBLAGE PATTERNS WITH RESPECT TO LANDSCAPE-SCALE HABITATS IN CENTRAL CALIFONIA

by Kristin I. Hunter-Thomson

In most ecosystems, the distribution of species across a landscape is greatly influenced by the type, amount, and spatial configuration of habitats. Studies in terrestrial environments have shown that species diversity, density, and length frequency often positively correlate with the size of a habitat patch, patch shape, and proximity to a patch edge. These patterns, however, have not been conclusively shown in temperate sub-tidal marine studies. Data from visual strip-transects collected from the *Delta* submersible were used to characterize fish assemblages with respect to rocky bank habitat patches. Specifically, the density, diversity, and length frequency of nearshore fishes were examined with respect to 1) proximity to the patch edge, 2) patch shape, and 3) patch size near Point Lobos and Point Sur, California. Diversity and length distributions of fishes were significantly greater at the edge than the interior of rocky bank patches. Therefore, landscape-scale patterns with respect to the distribution of nearshore fishes exist. However, this study also demonstrated that terrestrial paradigms are not directly applicable to temperate sub-tidal marine habitats. The relationship between species richness and patch shape was opposite of patterns observed in terrestrial systems. Additionally, patch size explained more of the variability in the nearshore fish assemblages than patch shape; however, neither were good predictive indicators of the density of fishes.

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Introduction

The spatial scales at which ecological processes occur vary (Wiens 1989, Risser 1995), ranging from smaller than tens of centimeters (e.g., Eggleston et al. 1998) to larger than hundreds of kilometers (e.g., Woodroffe and Ginsberg 1998). At a fine-scale, the distribution of individuals can be driven by habitat selection, species mobility, and prey availability among other things (Wiens 1976). For example, aquatic and marine studies have demonstrated associations between species distribution and lithology for many fishes and invertebrates (Osman 1977, Vannote and Minshall 1982, Ault and Johnson 1998, Wang et al. 2003, Anderson et al. 2005b). At an intermediate-scale, intra- and inter-specific interactions (Gosz 1993, Turner 2005) or habitat types (Kareiva 1990, Ciannelli et al. 2008) also can drive patterns in the distribution of assemblages. Finally at a broad-scale, the movement of energy and matter, through air and water (Turner 2005, Genin 2004) and across landforms (MacArthur and Wilson 1967), influences the distribution of populations across ecosystems.

Ecological processes at fine and broad scales are well investigated, but few studies of factors influencing ecological processes at intermediate, or landscape, scales exist. The field of landscape ecology was developed to gain an understanding of the patterns and processes that occur across landscapes. A landscape is defined as a distinct spatial area that contains multiple patches of different habitat types (Forman and Godron 1986, Turner 2005). In landscape ecology, the unit of measure is a habitat patch. Research in landscape ecology is characterized by studies of patterns of biotic processes at the assemblage and species level with respect to the spatial distributions of habitat patches (Forman and Godron 1981, Turner et al. 2001, Turner 2005). The scale of a landscape is defined as the scale that is relevant to a species' distribution or ecological processes of interest (Wiens 1989, Gosz 1993).

A habitat patch is defined as an area that differs from its surroundings, is relatively homogeneous, and has a distinct boundary (Forman 1995, Fagan et al. 1999). The distribution, orientation, and shape of habitat patches have been shown to influence the distribution of organisms (Forman and Godron 1986). Within a habitat patch, fine-scale habitat type variation exists. For example within a stream, the streambed can contain pebble and sand substrates, which can influence the distribution of organisms (Hynes 1970). Thus, some researchers have used the term habitat patch to define these fine-scale habitat type variations (e.g., pebble, sand) rather than the larger-scale habitat (e.g., the stream). However, this study uses the convention in landscape ecology to refer to the larger-scale habitat as the habitat patch (Kotliar and Wiens 1990).

Clear patterns in the assemblage structure of organisms with respect to landscape-scale habitat characteristics have been observed in terrestrial environments. For example, the density and diversity of the faunal assemblage in a habitat patch often correlates with three landscape-scale habitat characteristics: proximity to the edge of the habitat patch, habitat patch shape, and habitat patch size. First, species density and diversity have been shown to increase with proximity to the habitat patch edge, or at the ecotone (Odum 1958, Yahner 1988, Temple and Cary 1988). In addition, the abundance of larger individuals increases closer to the habitat patch edge (Connolly 1994). Second, habitat patches with more complex shapes have higher species density and diversity as well as a wider breadth of sizes of organisms (Kunin 1998, Fagan et al. 1999, Oksanen et al. 1992). Third, species density and diversity increase with increasing habitat patch area (van Dorp and Opdam 1987, Gosz 1993, Attrill et al. 2000).

Although these repeatable patterns between organisms and the environment are common on land, they have not been conclusively shown to occur in the marine environment. This is partially because ecological studies of species-habitat associations in the oceans have historically been focused at a smaller scale than in terrestrial studies. Most observations and experiments of marine species-habitat interactions have been conducted at the scale of centimeters to meters (e.g., Pearcy et al. 1989, Stein et al. 1992, Yoklavich et al. 2000, Heggenes and Saltveit 2007, Lindsay et al. 2008). Additionally, sub-tidal marine environments are remote and have been difficult to study. There is growing interest, however, in the value of understanding and quantifying the patterns in the distribution of organisms with respect to larger scale patches (hundreds of meters to kilometers; Kritzer and Sale 2006). Studies investigating the interactions between organisms and the marine environment across larger scales of the landscape are now being pursued more in the oceans (Wiens 1989, Irlandi 1994). Initial marine studies, though, have not shown a clear correspondence with terrestrial studies. Therefore, questions still remain about whether assemblage structures in the oceans are influenced by landscape-scale habitat characteristics in a similar manner as terrestrial assemblages. In addition, the majority of landscape-scale studies in the oceans has investigated patterns of distributions of invertebrates and fishes in seagrass meadows (e.g., Irlandi et al. 1999, Eggleston et al. 1999, Brooks and Bell 2001). Only a few studies have investigated patterns in invertebrate assemblage structure in temperate rocky bank habitats (e.g., Selgrath et al. 2007); no studies have examined patterns in fish assemblages with respect to landscape-scale habitat characteristics in temperate rocky bank habitats.

Rocky bank habitats are a common geological feature along the continental shelf of the US west coast in water depths of 0 – 200 m (Greene et al. 1999). Rocky habitats are comprised of fine-scale habitat types such as bedrock outcrops, pinnacles, rocky banks, and boulder fields. Unique assemblages of fishes are often observed in rocky bank habitats (Allen et al. 2006). These assemblages are primarily dominated by rockfish (*Sebastes* spp.) and have been described for central California by Love et al. (2002) and Love and Yoklavich (2006).

The objectives of this study were to determine if there are patterns in the assemblage structure of nearshore fishes with respect to landscape-scale habitat characteristics and whether or not these patterns persist across two regions of central California. In this study, the landscape-scale habitat patches investigated were rocky bank habitat patches (hereafter referred to as rocky bank patches), which occur at the scale of hundreds of meters in water depths of 30 – 100 m. Data from multi-beam sonar surveys was used to identify rocky bank patches and used observational data from submersible surveys to analyze patterns in the nearshore fish assemblage with respect to the spatial distribution and patterns of the rocky bank patches. The biological response variables that investigated were species density and biomass, diversity of the assemblage, and size composition. Patterns in these biological response variables were analyzed with respect to five independent habitat variables of the rocky bank patch: proximity to the edge, shape (as measured by the perimeter-to-area ratio, see methods), area, depth, and rugosity. Additionally, patterns in the density and lengths of four species groups and the seven most abundant species within the assemblage with respect to the independent habitat variables were compared to determine if certain species groups or species are the most important in determining observed assemblage patterns. Finally, patterns of the biological response variables of the assemblage with respect to the independent habitat variables were compared between two distinct regions (near Point Lobos and near Point Sur).

Background

Terrestrial Landscape Ecology

During the early 20th century, wildlife managers observed differences in species composition between the edge and the interior of habitat patches in terrestrial ecosystems (see summary by Turner 2005). The discovery of gradients in assemblage composition across a landscape resulted in an increased scientific interest in studying changes in ecological processes at the boundaries of habitat patches and the patterns of species distribution across landscapes. By the 1970s, terrestrial scientists had determined that the structure of the assemblage of organisms was a function of the type, availability, and spatial configuration of the habitat patches within the landscape (Forman and Godron

1986). Subsequent ecological studies have shown, for example, that the configuration of habitat patches in a landscape influences patterns of processes related to gene flow (Manel et al. 2003), population dynamics (Kareiva 1990), and assemblage structure (Wiens et al. 1993). Both Wiens (1976) and Saunders et al. (1991) provide reviews of the responses of populations to the spatial structure of landscapes, including changes in predation, competition, dispersal, and movement. Additionally, published studies have demonstrated differences in species-specific size and ontogenetic differences in distribution with respect to habitat-characteristics across a landscape (as summarized by Turner et al. 2001).

Predictable patterns of species distributions across a landscape have been attributed to distance from the edge of a habitat patch, habitat patch shape, and habitat patch area. Field experiments and theoretical models have shown that species density and diversity increase with proximity to the habitat patch edge, or at the ecotone (Yahner 1988, Temple and Cary 1988, Connolly 1994, Risser 1995, Fagan et al. 1999, Lidicker 1999, Bolger et al. 2000). Ward et al. (1999) highlighted that the magnitude of this increase in density with proximity to the habitat patch edge varies among species. Overall, the species diversity of an assemblage is elevated at the edge in comparison with the interior of the habitat patch. Furthermore, different species occur at the edge than at the interior of the habitat patch (Yahner 1988, Oksanen et al. 1992, Lidicker 1995, With and Crist 1995). Also, individuals of larger size of individual species are more frequently observed closer to the habitat patch edge than within the interior of a habitat patch

(Connolly 1994, Donovan et al. 1997, Yahner 1998, Tanner 2005, Turner 2005, Wilson et al. 2008).

Terrestrial studies also indicate that the shape of a habitat patch influences patterns in species distribution (Diamond 1975, Wilson and Willis 1975, Saunders et al. 1991, Golden and Crist 2000). Field experiments have illustrated that habitat patches with larger perimeter-to-area ratios have higher species density and diversity (Kunin 1998, Fagan et al. 1999, Bowden et al. 2001). These distributional patterns have been attributed to increases in foraging opportunities and other life history characteristics (Hawrot and Niemi 1996). Additionally, the size structures of different species vary with habitat patch shape. Habitat patches with greater perimeter-to-area ratios have a wider breadth of sizes of organisms than habitat patches with smaller ratios (Oksanen et al. 1992).

The area of a habitat patch also influences the density and diversity of an assemblage. Species diversity and richness increase with increases in habitat patch area (Gosz 1993, Attrill et al. 2000, Bolger et al. 2000, Hovel et al. 2002, Heegaard et al. 2007). However, not all species respond similarly to the change in habitat patch size. For example, Bender et al. (1998) summarized how different species respond to patch sizes; they reported that edge- and interior-specific species are more influenced by changes in patch size than generalist species. Additionally, the literature is currently divided about whether increases in patch size result in an increase or decrease in species density (see review by Bowman et al. 2002). In fact, Bowers and Matter (1997) determined that the density-area relationship was scale dependent; negative density-area relationships are observed in small-scale habitat patches whereas positive relationships occur in large-scale habitat patches.

Marine Landscape Ecology

Marine scientists have begun to ask landscape-scale ecological questions, especially related to assemblage structure in seagrass, coral reef, and rocky habitats (Wiens 1989, Irlandi 1994, García-Charton et al. 2004). The early studies, which described patterns in species distribution with respect to landscape-scale habitat characteristics, have shown evidence both in support of and in opposition to the patterns observed in terrestrial studies. A variety of studies has examined terrestrial paradigms in eelgrass patches. For example, species density and diversity increased both with edge proximity (Irlandi 1994, Friedlander and Parrish 1998, Bologna and Heck 2002) and increasing marine patch shape complexity (Irlandi 1997, Eggleston et al. 1999, Hovel and Lipcius 2001). Also, an investigation of the patterns of species distribution on reef patches described a positive correlation of species density and diversity to edge proximity and higher perimeter-to-area ratios (Selgrath et al. 2007). In one study, the size structure of fish assemblages also changed with habitat patch shape (Irlandi et al. 1995). Finally, Bowden et al. (2001) observed increases in the total number of taxa in seagrass patches of greater area.

Several other studies, however, have reported marine landscape patterns that contradict those predicted from terrestrial landscape ecology, indicating a need to investigate landscape-scale questions further in marine systems. Jelbart et al. (2006) determined that diversity of fishes decreased with proximity to the edge of an eelgrass patch due to increased predation rates. Hovel et al. (2002) observed no clear pattern in the relationship between species density and eelgrass patch shape. Similarly, García-Charton et al. (2004) observed positive, negative, and non-linear relationships between fish species abundance and reef patch size as well as no relationship among species biomass and landscape-scale habitat characteristics. Additionally, Johnson et al. (1994) determined that suitable prey were substantially more abundant within the reef patch than in adjacent sand patches for four reef fishes in southern California, suggesting that the edge of a reef patch did not provide the presumed increase in foraging opportunities for predators. Baltz et al. (1993) and Eggleston et al. (1998) illustrated that the patterns of species density across a landscape were influenced by the size of the marsh fishes and macro-fauna sampled rather than the habitat characteristics of the landscape.

The ability to model marine systems using patterns observed in terrestrial systems is increasingly being questioned. For example, Hovel et al. (2002) observed that the distribution of faunal densities is influenced by many covarying environmental factors, at multiple spatial scales in eelgrass meadows, and these relationships change seasonally. They suggested that because the number of factors that vary are greater in marine environments than on land they were unable to replicate terrestrial patterns in their study. In addition, Carr et al. (2003) summarized differences between terrestrial and marine systems that result in altered patterns in the structure and dynamics (spatial, genetic, and trophic) of the biology of marine environments (see Table 1 in Carr et al. 2003). They attribute these differences in patterns at the assemblage, population, and ecosystem levels to the greater "openness" of marine systems. Hovel et al. (2002) and Carr et al. (2003) emphasized the need to investigate whether terrestrial paradigms are applicable to marine systems despite these differences.

To date, landscape-scale studies examining patterns of species distribution in marine landscapes have been focused on estuaries and tropical reefs. Ebeling and Hixon (1991) reviewed the differences in the structure of fish assemblages and causes for the differences between tropical and temperate reefs, indicating that patterns observed in tropical ecosystems may not apply to temperate ecosystems. Additionally, only a few studies have investigated questions regarding fish-habitat relationships with respect to landscape-scale habitat characteristics in the temperate, sub-tidal marine system. As Anderson et al. (2005a) and Anderson and Yoklavich (2007) identified, the lack of knowledge of the ecological processes at larger scales limits the effectiveness of local fisheries management in temperate regions because there is a disconnect between the scale of the data (tens of meters) and the scale needed for management (hundreds of meters to kilometers).

In situ Fish Surveys

Human-occupied submersible surveys have proven to be an effective technique for surveying nearshore fish populations in deep water (see Yoklavich and O'Connell 2008). The use of a submersible enables researchers to observe fishes in their natural habitat. From the data collected, scientists can calculate the density and diversity of demersal fishes (e.g., Stein et al. 1992, Yoklavich et al. 2000). Additionally, fine-scale habitat data can be recorded, often following the protocol proposed by Greene et al. (1999), thus enabling researchers to identify fish-habitat associations.

Data collected from *in situ* surveys also can be used for analyses of the assemblage structure of fishes and of the relationship between the fish assemblage and the surrounding habitat patch. By utilizing multiple surveys throughout an area that align with the scale of subpopulations or the home ranges of multiple species, researchers can describe relationships among the assemblage structure and the heterogeneity of the habitat patches at a landscape scale. In combination with current seafloor maps, data from a human-occupied submersible was used to quantify the assemblage structure and relevant landscape-scale habitat characteristics along the central coast of California. The data used included fish species' presence, abundance, and size as well as the geographic location of each observed fish. Using these techniques, this study provides the first in-depth investigation of patterns in temperate sub-tidal fish assemblages with respect to the landscape-scale spatial structure of the rocky bank landscape.

Materials and Methods

Submersible Surveys and Study Sites

Data for this study were collected in 2004, 2007, and 2008 using a human-occupied submersible, the *Delta*. In 2004, surveys were conducted to develop a baseline assessment of the densities and species composition of rockfishes and other nearshore fishes within the newly established Rockfish Conservation Areas (PFMC 2009). During fall 2007 and 2008, submersible surveys were conducted to collect baseline assessments of nearshore fish and macro-invertebrate assemblages inside and adjacent to nine Marine Protected Areas (MPAs) in central California, which were established in September 2007 (Starr and Yoklavich 2008).

Data were collected following similar techniques as described in Yoklavich and O'Connell (2008). Ten-minute visual strip transects that were two meters wide and on average 236 m long (range 41 – 402 m) were conducted to count fishes and invertebrates, characterize fine-scale habitat types, and collect video records. Fishes were identified to the lowest taxonomic level possible, most often to species. A few adjustments to the techniques described by Yoklavich and O'Connell (2008) were used to collect the data for this study. For example in 2007 and 2008, a Doppler Velocity Log was attached to the submersible, which provided a more accurate estimate of the distance traveled than that obtained from the Track-point and WinFrog navigation systems or the laser count methods previously used. Tissot (2008) provided a summary of the at-sea and land-based data preparation and processing techniques used for data collected from the 2007 and 2008 submersible surveys.

Data from these projects were opportunistically used for this study. All fish survey transects that occurred within the designated rocky bank patches were included in the study. When necessary, the original fish transects were truncated to remove portions outside of the rocky bank patches. Therefore, the mean fish transect distance used in this study was 199 m (range 8 – 351 m). Each of the rocky bank patches contained between 3 and 9 fish transects.

In this study, the data used were collected from two regions of the central California coast: near Point Lobos (36°31'19.8" N 121°57'9.0" W) and near Point Sur (36°18'20.5" N 121°53'57.0" W; Fig. 1). Within these two regions, this study focused on the assemblage structure of fishes in the mid-depth rocky habitat from 30 – 100 m. Allen et al. (2006) identified this depth zone as a faunal break for nearshore fish assemblages.[1] While these two regions are in close proximity (roughly 50 km apart), each has distinct characteristics that may influence the habitats and fish distributions. For example, each region is composed of different bedrock types; Point Lobos is porphyritic granodiorite while Point Sur is metamorphic sandstone (Blake and Jones 1981, Norris and Webb 1990, Davidson et al. 2002). Point Lobos contains multiple canyon heads, whereas Point Sur is a large gradually slooping shelf (Fig. 1).

[1] Allen et al. (2006) describes this faunal assemblage within 30 – 100 m as the "mid-depth rocky habitat" group, whereas Love et al. (2002) classifies the species group of rockfishes in the same depth range as the "shallow shelf" assemblage.

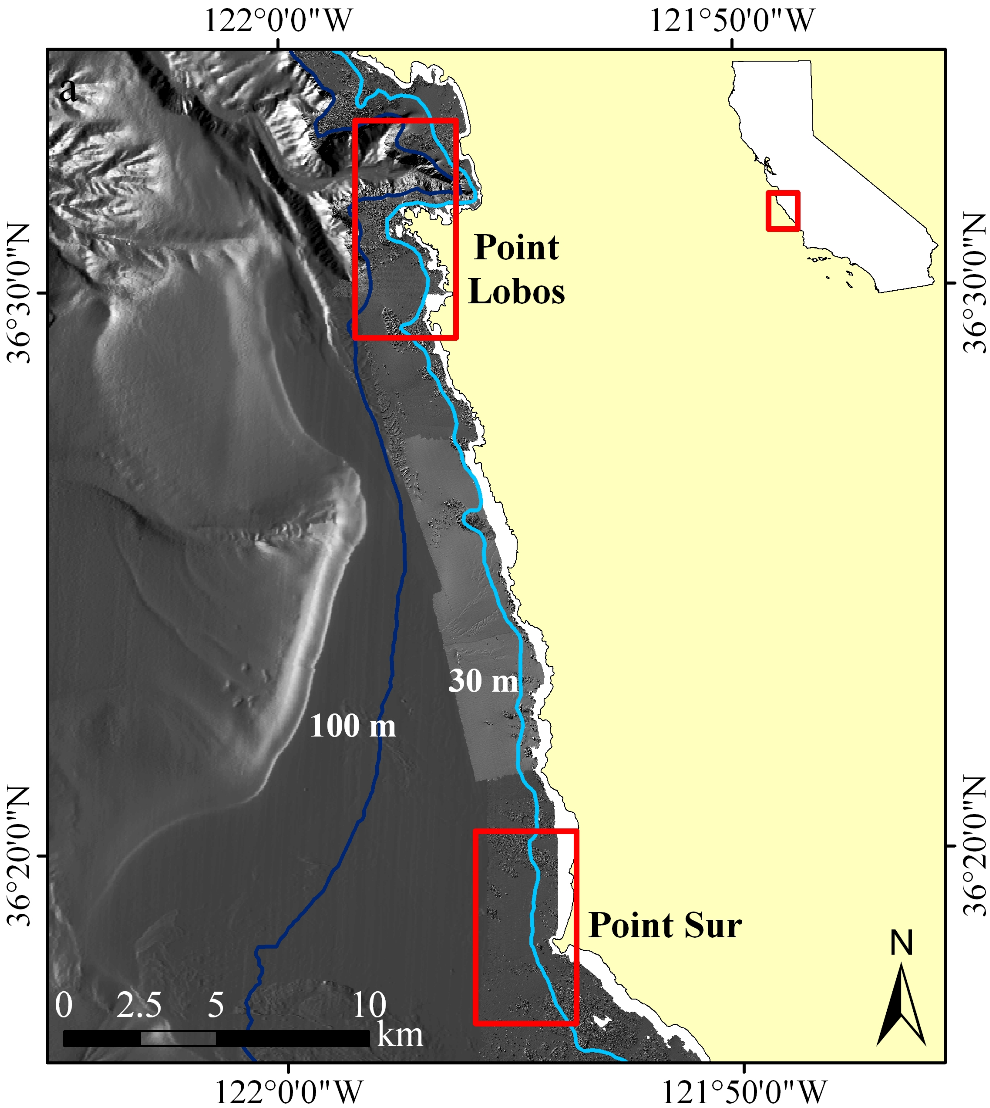


Fig. 1 Map of the study region highlighting the two focus regions: Point Lobos and Point Sur. The red boxes denote the regions in which the rocky bank patches included in this study occurred. The blue lines represent the 30 m (light blue) and 100 m (dark blue) isobaths. The seafloor bottom topography is depicted based on the 2-m side scan sonar images

Independent Habitat Variables

This study investigated landscape patterns at 37 rocky bank patches across the central coast: 24 near Point Lobos and 13 near Point Sur. Two criteria were used to classify a rocky bank patch: the amount of fine-scale habitat and the sharpness of habitat changes at the boundary. For the first criterion, only rocky bank patches that were predominantly (> 80%) rocky habitat (e.g., rock outcrop, boulder) were used. Second, at least 75% of the boundary of each patch had to abut a major change in habitat type (e.g., the habitat changed abruptly from rock to sand). Following these criteria, 2-m resolution side-scan sonar images loaded into ArcGIS were used to define and delineate the rocky bank patches within the study sites (Fig. 2a-b). All the rocky bank patches contained similar fine-scale habitat types. Rocky bank patches were distributed throughout the selected 30 – 100 m depth range near Point Lobos, but were restricted to shallow depths near Point Sur (< 55 m). The mean rocky bank patch diameter was 288 m (range 114 – 714 m; Fig. 3).

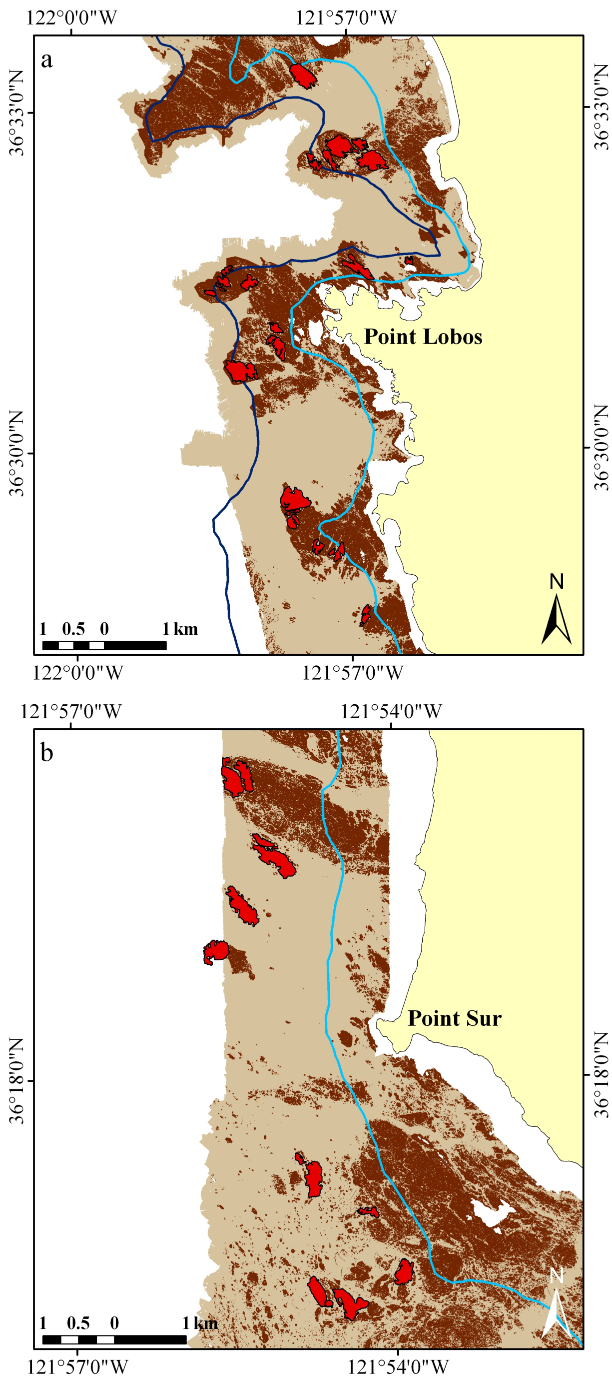


Fig. 2 Distribution of selected rocky bank patches near Point Lobos and Point Sur. The red polygons represent the rocky bank patches analyzed in this study (n = 37). The blue lines represent the 30 m (light blue) and 100 m (dark blue) isobaths. Areas in light tan represent soft sediment and dark brown areas represent hard bottom habitat based upon GIS substrate layers from CSUMB Seafloor Mapping Lab

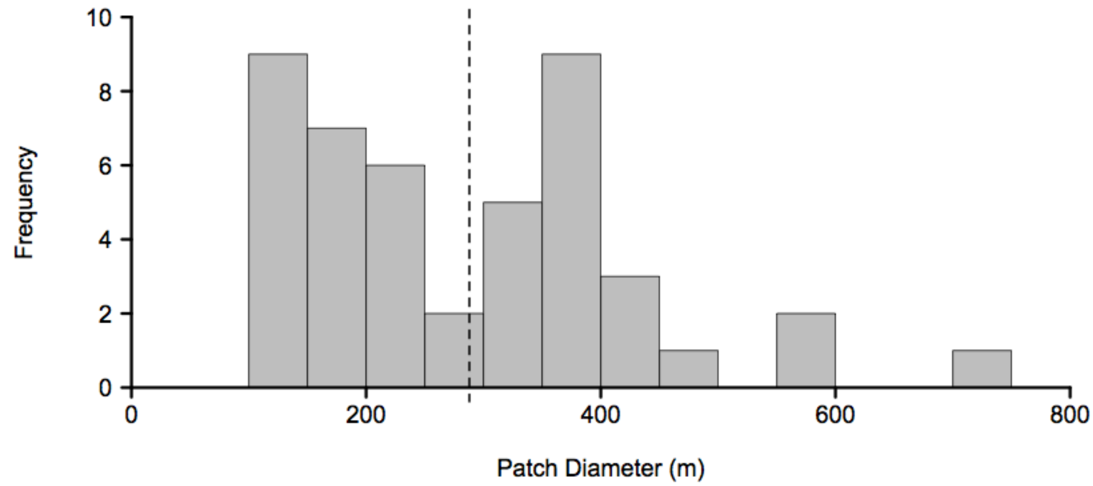


Fig. 3 Frequency histogram of rocky bank patch diameters near Point Lobos and Point Sur. Dotted line denotes the mean rocky bank patch diameter (228 m)

The five independent habitat variables that this study evaluated for the selected rocky bank patches were: proximity to the edge of a patch, patch shape, patch size, patch depth, and patch rugosity (Table 1). The edge of the rocky bank patch was defined as a zone containing rock at the outer perimeter of the rocky habitat, thus excluding soft sediment habitats adjacent to the rocky bank patch. To determine an appropriate width for the edge zone, sections of fish transects were assigned as edge or non-edge iteratively using 2 m increments between 2 and 40 m from the rocky bank patch boundary. For each width of edge zone, the density and richness per unit area of fishes along fish transects were calculated. A natural break point in the data, as defined by a change in the slope, was used as an objective measure to determine an appropriate edge zone width. To quantify differences between edge and interior areas of a rocky bank patch, a buffer between the edge and interior zones was used to separate them in space, thus reducing spatial autocorrelation. To be conservative, a buffer width that was twice the width of the edge zone was used. Data along fish transects that occurred within the buffer were removed from proximity to edge analyses.

Table 1 List of hypotheses and observed results. The hypotheses and observed results are for assemblage level analyses (a), species-group analyses (b), species-specific analyses (c), and regional comparison assemblage analyses (d). Hyp are the hypotheses and Obs are the observed results. The + represents a positive relationship, - represents a negative relationship, ns means there was no significant relationship, S denotes shallow patches, and D denotes deep rocky bank patches

a - Assemblage	**Depth**		**Rugosity**		**Distance to Edge**		**Patch Shape**		**Patch Size**	
	Hyp	*Obs*	*Hyp*	*Obs*	*Hyp*	*Obs*	*Hyp*	*Obs*	*Hyp*	*Obs*
Density	+	+	+	ns	+	ns (S & D)	+	ns	+	ns
Biomass	+	+	+	ns	+	ns (S & D)	+	ns	+	ns
Richness	+	ns	+	ns	+	+	+	-	+	+
Evenness	+	-	+	ns	+	+ (S & D)	+	ns	+	ns
Heterogeneity	+	-	+	ns	+	+ (S & D)	+	ns	+	ns

b - Species Groups	**Depth**		**Rugosity**		**Distance to Edge**		**Patch Shape**		**Patch Size**	
	Hyp	*Obs*	*Hyp*	*Obs*	*Hyp*	*Obs*	*Hyp*	*Obs*	*Hyp*	*Obs*
Density										
large rockfishes	+	+	+	ns	+	ns (S), + (D)	+	ns	+	ns
dwarf rockfishes	+	+	+	ns	+	ns (S), + (D)	+	ns	+	ns
large non-rockfishes	+	ns	+	ns	+	ns	+	ns	+	ns
other benthic fishes	-	+	+	+	+	+ (S), ns (D)	+	ns	+	ns
Length Distribution										
large rockfishes	+	ns	+	ns	+	ns	+	ns	+	ns
dwarf rockfishes	+	+	+	- (S), + (D)	-	- (S), + (D)	-	+ (S & D)	+	- (S), + (D)
large non-rockfishes	+	ns	+	N/A	+	ns	+	ns	+	ns
other benthic fishes	+	ns	+	ns	+	ns	+	ns	+	ns

Table 1 cont.

c - Specific Species	Depth		Rugosity		Distance to Edge		Patch Shape		Patch Size	
	Hyp	*Obs*	*Hyp*	*Obs*	*Hyp*	*Obs*	*Hyp*	*Obs*	*Hyp*	*Obs*
Density										
Blackeye Goby	-	-	-	ns	+	ns (S), + (D)	+	ns	+	ns
Blue Rockfish	+	-	+	-	+	ns	+	ns	+	ns
Painted Greenling	-	-	+	+	+	ns	+	ns	+	ns
Pygmy Rockfish	+	+	-	ns	+	ns	+	ns	+	ns
Rosy Rockfish	+	+	+	ns	+	ns	+	ns	+	ns
Squarespot Rockfish	+	+	+	ns	+	ns	+	ns	+	ns
Starry Rockfish	+	+	+	ns	+	ns	+	ns	+	ns
Biomass										
Blackeye Goby	-	-	-	ns	+	ns (S), + (D)	+	ns	+	ns
Blue Rockfish	+	ns	+	ns	+	ns	+	ns	+	+
Painted Greenling	-	-	+	+	+	ns	+	ns	+	ns
Pygmy Rockfish	+	+	-	+	+	ns	+	ns	+	ns
Rosy Rockfish	+	+	+	ns	+	ns	+	ns	+	ns
Squarespot Rockfish	+	+	+	ns	+	ns	+	ns	+	+
Starry Rockfish	+	+	+	ns	+	ns	+	ns	+	+
Mean Length										
Blackeye Goby	-	-	-	ns	+	+ (S & D)	+	ns	+	ns
Blue Rockfish	-	ns	+	ns	+	ns	+	ns	+	ns
Painted Greenling	-	-	+	+	+	ns	+	ns	+	ns
Pygmy Rockfish	+	+	-	ns	+	ns (S), + (D)	+	ns	+	ns
Rosy Rockfish	+	+	+	ns	+	+ (S & D)	+	ns	+	ns
Squarespot Rockfish	+	+	+	ns	+	ns (S), + (D)	+	ns	+	+
Starry Rockfish	+	+	+	ns	+	ns (S), + (D)	+	ns	+	+
Length Distribution										
Blackeye Goby	-	ns	-	ns	+	ns	+	ns	+	ns
Blue Rockfish	-	ns	+	ns	+	ns	+	ns	+	ns
Painted Greenling	-	ns	+	ns	+	ns	+	ns	+	ns
Pygmy Rockfish	+	+	-	+ (S & D)	+	ns	+	ns (S), + (D)	+	ns (S), + (D)
Rosy Rockfish	+	ns	+	ns	+	ns	+	ns	+	ns
Squarespot Rockfish	+	ns	+	ns	+	ns	+	+	+	+
Starry Rockfish	+	ns	+	ns	+	ns	+	ns	+	ns

Table 1 cont.

d - Regional Comparison		Distance to Edge		Patch Shape		Patch Size	
		Hyp	*Obs*	*Hyp*	*Obs*	*Hyp*	*Obs*
Density							
	Point Lobos	+	ns	+	ns	+	ns
	Point Sur	+	ns	+	ns	+	ns
Biomass							
	Point Lobos	+	ns	+	ns	+	ns
	Point Sur	+	ns	+	ns	+	ns
Richness							
	Point Lobos	+	ns	+	-	+	+
	Point Sur	+	ns	+	ns	+	ns
Evenness							
	Point Lobos	+	+	+	ns	+	ns
	Point Sur	+	ns	+	ns	+	ns
Heterogeneity							
	Point Lobos	+	+	+	ns	+	ns
	Point Sur	+	ns	+	ns	+	ns

The second and third independent habitat variables were the rocky bank patch shape and patch size. Using ArcGIS Hawth's Tools extension the perimeter and area for each rocky bank patch was deteremined. The perimeter-to-area (P:A) ratio was calculated for each rocky bank patch by dividing the perimeter by the area. This ratio measurement was used as a quantitative proxy for the patch shape. When necessary, area and P:A ratio data were binned to create two discrete categories using the mean value as the break point for both area and P:A ratio.

The fourth and fifth habitat characteristics of the rocky bank patches analyzed were patch depth and patch rugosity. Mean depth per rocky bank patch was calculated from the Seabird SBE19 Plus Seacat Profiler instrument attached to the submersible. For some analyses, depth was used to separate the data into two categories. Shallow patches included rocky bank patches in less than 55 m of water depth and deep rocky bank patches in waters greater than 65 m deep. These depth bins were chosen to ensure equal sample size between the shallow and deep portions of the data set. ArcGIS data layers of rugosity, from the CSUMB Seafloor Habitat Mapping Lab, were used to determine the rugosity value for each position along the fish transects and for the rocky bank patches as a whole. Rugosity is often calculated as the non-dimensional relationship between the surface area of the seafloor and the linear surface area (Luckhurst and Luckhurst 1978); CSUMB uses digital elevation models to calculate the rugosity from high-resolution multi-beam bathymetry. Rugosity levels in the rocky bank patches range from 1.025 – 1.364; low rugosity was defined as values that ranged from 0 to 1.182 and high rugosity as values greater than 1.182. These divisions of low and high rugosity categories were chosen because they correspond with the rugosity values of fine-scale habitat types observed during the submersible surveys.

Biological Response Variables

Patterns of the fish assemblage were analyzed at three different levels of biological organization: all fishes combined to represent the entire assemblage, fishes separated into four species groups, and individual patterns for the seven most abundant species. Assemblage analyses were evaluated for all species observed on fish transects. A subset of species was assigned to the four species groups by a combination of taxonomy, size, and habitat association. The species groups include: “large” rockfishes (*Sebastes* spp.), dwarf rockfishes (*Sebastes* spp.), “large” non-rockfishes, and other benthic fishes (see Table 2 for list of the species comprising each group). The seven most abundant fishes observed on transects were used for species-specific analyses. These seven species were chosen because they individually comprised more than 1% of the total abundance of all fishes observed (Appendix A). Although the independent habitat variables used in this study may influence common and rare species differently (Wiens 1976), there were insufficient data to test patterns of rare species with respect to the independent habitat variables.

Table 2 Species that comprise each of the four species groups used for the species-group analyses. The published maximum total length per species is reported. Species were chosen based upon a similarity of taxonomy, size, and habitat associations

Species Group	Scientific Name	Common Name	Maximum Total Length
large rockfishes	*Sebastes caurinus*	Copper Rockfish	66 cm
	Sebastes constellatus	Starry Rockfish	46 cm
	Sebastes miniatus	Vermilion Rockfish	76 cm
	Sebastes paucispinis	Bocaccio	91 cm
	Sebastes pinniger	Canary Rockfish	76 cm
	Sebastes ruberrimus	Yelloweye Rockfish	91 cm
dwarf rockfishes	*Sebastes hopkinsi*	Sqaurespot Rockfish	29 cm
	Sebastes rosaceus	Rosy Rockfish	58 cm
	Sebastes semicinctus	Halfbanded Rockfish	25 cm
	Sebastes wilsoni	Pygmy Rockfish	23 cm
large non-rockfishes	*Hydrolagus colliei*	Pacific Ratfish	97 cm
	Ophiodon elongatus	Lingcod	152 cm
other benthic fishes	*Hexagrammos decagrammus*	Kelp Greenling	61 cm
	Oxylebius pictus	Painted Greenling	25 cm
	Scorpaena guttata	California Scorpionfish	43 cm
	Sebastes atrovirens	Kelp Rockfish	42.5 cm
	Sebastes carnatus	Gopher Rockfish	42.5 cm

Seven biological response variables were used to define the structure of the nearshore fish assemblage: richness, evenness, heterogeneity, density, biomass, mean length, and length frequency distribution (Table 2). The assemblage diversity indices (richness, evenness, and heterogeneity) were only calculated for the assemblage. For the diversity indices, the species richness, evenness (Pielou's evenness index), and heterogeneity (Shannon-Wiener diversity index; Appendix C) were calculated. Density was calculated for the assemblage, species groups, and seven specific species. Density was calculated as the mean number of fishes per 10 m^2 of area surveyed along each fish transect. Fish biomass of the assemblage and seven specific species, which also was averaged along each fish transect, was calculated using the Fish Biomass Conversion Equation ($W = a*L^b$; Anderson and Gutreuter 1983) and the collected size and frequency data. Published total length and total weight parameters (a and b) for each species, or the most closely related species available, were used (Appendix B). Finally, the size structure of fishes was investigated using the both the mean length (seven specific species) and length frequency distributions (species groups and seven specific species). The length data were originally collected in 5 cm bins of the total lengths of fishes, thus the length frequency analyses were conducted in 5 cm increments.

Analytical Techniques

First, patterns among the biological response variables were investigated at the assemblage level with respect to the independent habitat variables near Point Lobos. To determine if these assemblage patterns were driven by specific species within the assemblage, patterns in the biological response variables were then investigated for the four species groups and seven specific species with respect to the independent habitat variables. Finally, a comparison of the observed patterns in the structure of the nearshore fish assemblages near Point Lobos with those observed near Point Sur was conducted. All analyses were conducted using the software package R.

Analyses were made using rocky bank patches as the sample unit, with individual fish transects within a patch as the subsamples of the rocky bank patch. Fish density, biomass, and mean length data were averaged across the subsamples. The richness, evenness, heterogeneity, and length frequency data were cumulative calculations among the subsamples. Analyses of patterns among the biological response variables and all independent habitat variables followed these methods. For all analyses an alpha of 0.05 was used to determine statistical significance.

Previous studies have reported that the structure of fish assemblages correlates with depth and rugosity. Therefore, the relationship among the biological response variables with depth and then rugosity was investigated prior to analyzing the other independent habitat variables. If there was a significant relationship among a biological response variable with depth this relationship was accounted for in further analyses. These analyses were either conducted by comparing the biological response variable data in bins, shallow and deep categories, or the residuals of depth and the biological response variable with the independent habitat variable. Additionally, prior to analyzing the patterns of the biological response variable with respect to the proximity to edge, patch shape, or patch size, the relationship between the biological response variable and rugosity was analyzed, after accounting for depth. Using binned or residual data it was possible to ensure that the effect of depth did not mask the effects of other independent habitat variables on the biological response variables. Appendix D includes the distribution of rocky bank patches across depth zones and rugosity levels.

Density, Biomass, and Abundance Analyses. Linear regressions and ANOVAs were performed to investigate the relationships among the density of fishes (dependent variable) and each independent habitat variable. All of the following analyses were repeated for each independent habitat variable. Linear regressions were used to test for a relationship between the continuous habitat data (depth, rugosity, patch shape, and patch size) and fish density and biomass. For these analyses, the density data, or when necessary, the residuals of depth with density, was used to test the relationship with each independent habitat variable. ANOVAs were used to investigate patterns in density with respect to proximity to the edge of a rocky bank patch. If necessary, the data were split for each biological response variable by depth category. Then the analyses were conducted on the relationship between proximity to edge and density separately for each depth zone. A significant difference in density between the edge and interior zones of a rocky bank patch would indicate the presence of an edge effect.

Patterns in density at the assemblage level could mask more detailed responses of specific species density with respect to each independent habitat variable. Therefore, regression and ANOVA analyses were repeated for both the four species groups and then the seven most abundant species to compare the species group and species-specific patterns of density with respect to each independent habitat variable. All of the above analyses were repeated for biomass of the assemblage and the seven most abundant species.

To determine if the abundances of the four species groups were distributed proportionally with respect to the independent habitat variables, a Preference Index (Krebs 1999) and Goodness-of-Fit (Quinn and Keough 2002) analyses were used. The Preference Index estimated the expected abundance, which was set at an equal distribution between the independent habitat variable categories. This represents the utilization of habitat by fishes, rather than a true test of the preference of a species for a specific habitat type. The Goodness-of-Fit analyses compared the observed and expected abundances against the categories of proximity to edge, rocky bank patch shape, and rocky bank patch size. The independent habitat variables were binned into two categories based upon the mean value. These tests were used to determine if the species groups were proportionally distributed across each independent habitat variable category, i.e., if species associated more strongly with certain habitat characteristics.

Assemblage Diversity Analyses (Richness, Evenness, and Heterogeneity). Statistical tests similar to those described above were used to compare species composition of the assemblage, in terms of richness, evenness, and heterogeneity, to the independent habitat variables. The Bray-Curtis Index of Similarity was used to determine the similarity matrix among the species composition across depth categories, proximity to edge categories, and locations. This metric is not sensitive to sample size, species diversity, or proportional differences in abundance but is able to detect additive changes to the species composition of an assemblage (Krebs 1999). The index ranges from 0, which is no similarity, to 1, which is complete similarity; for this study 0.6 was used as the threshold for similarity between assemblages, based off of the upper similarity range reported by Cailliet and Barry (1979).

Mean Length and Length Frequency Distribution Analyses. The final biological response variable investigated was the length of individuals for the species groups and the seven specific species. Both the mean length and length frequency distributions were used for analyses of the seven specific species, but only the length frequency distributions for the species groups. Linear regressions were used to determine if there were relationships between the mean lengths of fishes and each independent habitat variable. ANOVAs were used to investigate patterns in the mean length of each species between the edge and interior zones of a rocky bank patch. Also, the length frequency distributions in relation to each independent habitat variable were compared using Kolmogorov-Smirnov tests. These values were calculated by determining the cumulative length frequencies of each species within a rocky bank patch across transects. The cumulative values then were averaged across rocky bank patches for each independent habitat variable.

Regional Comparison Analyses. All of the statistical analyses conducted for the biological response variables of the assemblage in shallow rocky bank patches near Point Lobos were repeated for the assemblage data near Point Sur. Only the shallow rocky bank patches were used for the regional comparisons due to sample size constraints. The same edge distance as defined for Point Lobos was used in Point Sur. The results and patterns in the biological response variables with respect to the independent habitat variables were compared between the locations to determine if patterns were consistent between two regions in central California.

Other Analyses. Species accumulation curves were compiled for each depth category near Point Lobos and for shallow rocky bank patches near Point Sur (Appendix E). Additionally, the standard error and coefficient of variation for assemblage fish density with respect to sample size were analyzed to further ensure a robust sample size (Appendix E). Using the method described by Bizzarro et al. (2007), the slope among the final four points of each curve was calculated to determine if an asymptote was reached (Appendix E). Numerous studies have documented species-area relationships; therefore, the data were resampled to calculate the cumulative number of species (S) across fish transects as well as among the rocky bank patches. Results from the resampling analyses were compared with predicted values derived from the species-area relationship equation, $S = c*A^z$ (Arrhenius 1921 summarized in Gotelli 2001), where A is area, and c and z are fitted coefficients. Additionally, the data were resampled to calculate the cumulative abundance of species observed across fish transects as well as among the rocky bank patches.

Results

Species Abundance and Composition

During the fish transects used for this study, 38,845 fishes were identified and enumerated. A total of 68 fish taxa was recorded within the sample area and 58 of those were identified to the species level (Appendix A). Of the observed fishes, *Sebastes* was the dominant genus within the assemblage (representing 50% of the taxa and 79.4% of the total abundance). A total of 8,156 fishes (26.3% of the total abundance) was recorded in the generic "rockfish"[2], sub-generic "*Sebastomus*", or the "unidentified" categories. These fishes were used for the assemblage analyses but not for the species groups or species-specific analyses. Near Point Lobos, 11 taxa accounted for > 1% of the total abundance; near Point Sur, 13 taxa accounted for > 1% (Appendix A). To compare species-specific patterns, the most abundant species from Point Lobos were used. The species, in descending order, included Pygmy Rockfish (*Sebastes wilsoni*, Gilbert 1915), Blackeye Goby (*Rhinogobiops nicholsii*, Bean 1882), Squarespot Rockfish (*S. hopkinsi*, Cramer 1895), Rosy Rockfish (*S. rosaceus*, Girard 1854), Blue Rockfish (*S. mystinus*, Jordan and Gilbert 1881), Widow Rockfish (*S. entomelas*, Jordan and Gilbert 1880), Painted Greenling (*Oxylebius pictus*, Gill 1862), Starry Rockfish (*S. constellatus*, Jordan and Gilbert 1880), and Olive Rockfish (*S. serranoides*, Eigenmann and Eigenmann

[2] Following data collection protocols fish are included in the "rockfish" category if they are from the genus *Sebastes* but the observer is unable to identify the species or if the defining markings of the subgenus *Sebastomus* were not visible.

1890). Widow and Olive Rockfish were not included in the analyses of the most abundant species because they are mid-water species that are less associated with the bottom habitats included in the submersible surveys. Therefore, only 7 species were used for the species-specific analyses.

Defining the Edge Width

The density of all fishes per unit area surveyed decreased rapidly with increasing edge widths until around 12 m; adding additional edge width did not result in a substantial change in the density per unit area surveyed (Fig. 4a). Similarly, the richness per unit area surveyed decreased rapidly with increasing edge width until it leveled off around 12 m (Fig. 4b). Additionally, the mean richness per unit area surveyed was 0.028, which occurred at 12 m. Therefore, the edge width zone was defined as the first 12 m from the rocky bank patch boundary. Data for the interior zone included fishes that were observed at distances greater than 36 m from the rocky bank patch boundary. All fishes observed between 12 m and 36 m from the rocky bank patch boundary were removed from analyses to spatially separate the edge and interior zones of the rocky bank patch.[3]

[3] Forty-two percent of the observed fish on fish transects were observed within the buffer zone of rocky bank patches.

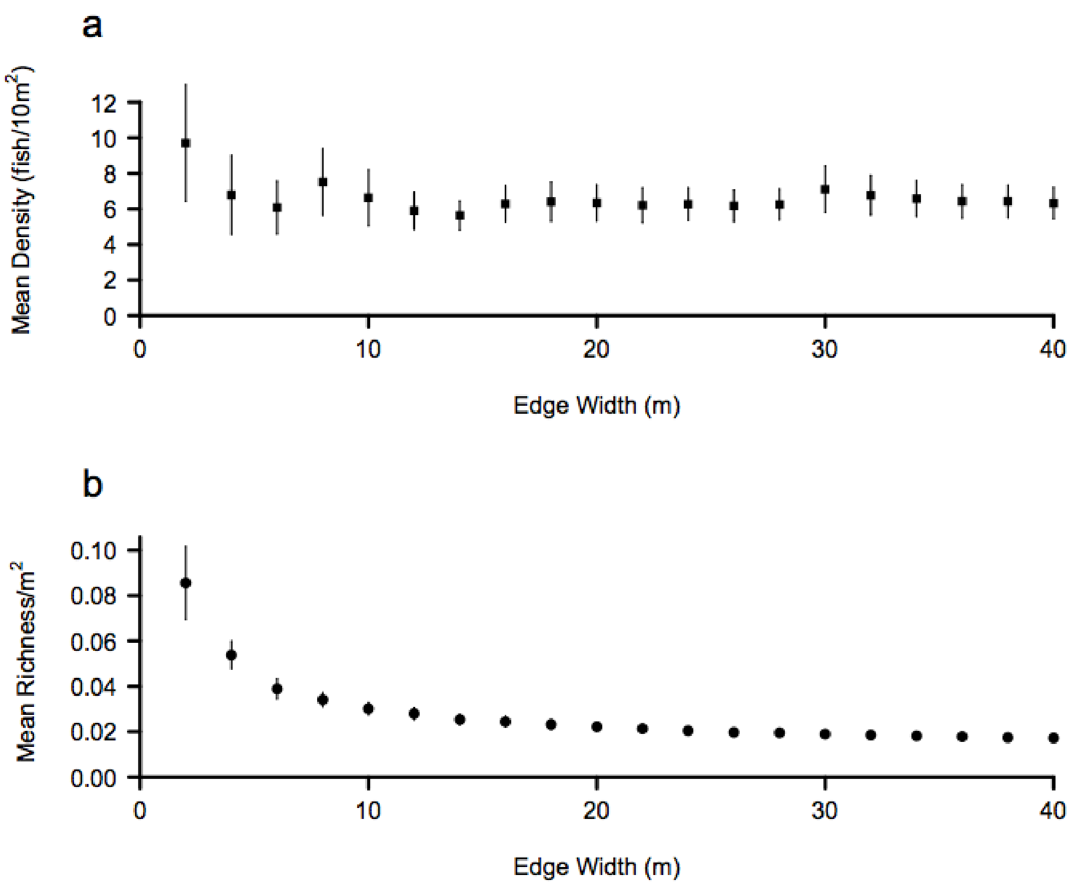


Fig. 4 Assemblage density and richness per unit area surveyed at different widths of the edge zone. Density (a) and richness (b) per unit area surveyed of the nearshore fish assemblage were calculated for each incremental cumulative 2 m width of edge zone from 2 – 40 m. Standard error is plotted as vertical bars

Assemblage Analyses

Depth and Rugosity. The fish assemblage structure varied with respect to depth. The overall species composition similarity index between shallow and deep patches near Point Lobos was only 0.493 (Fig. 5).

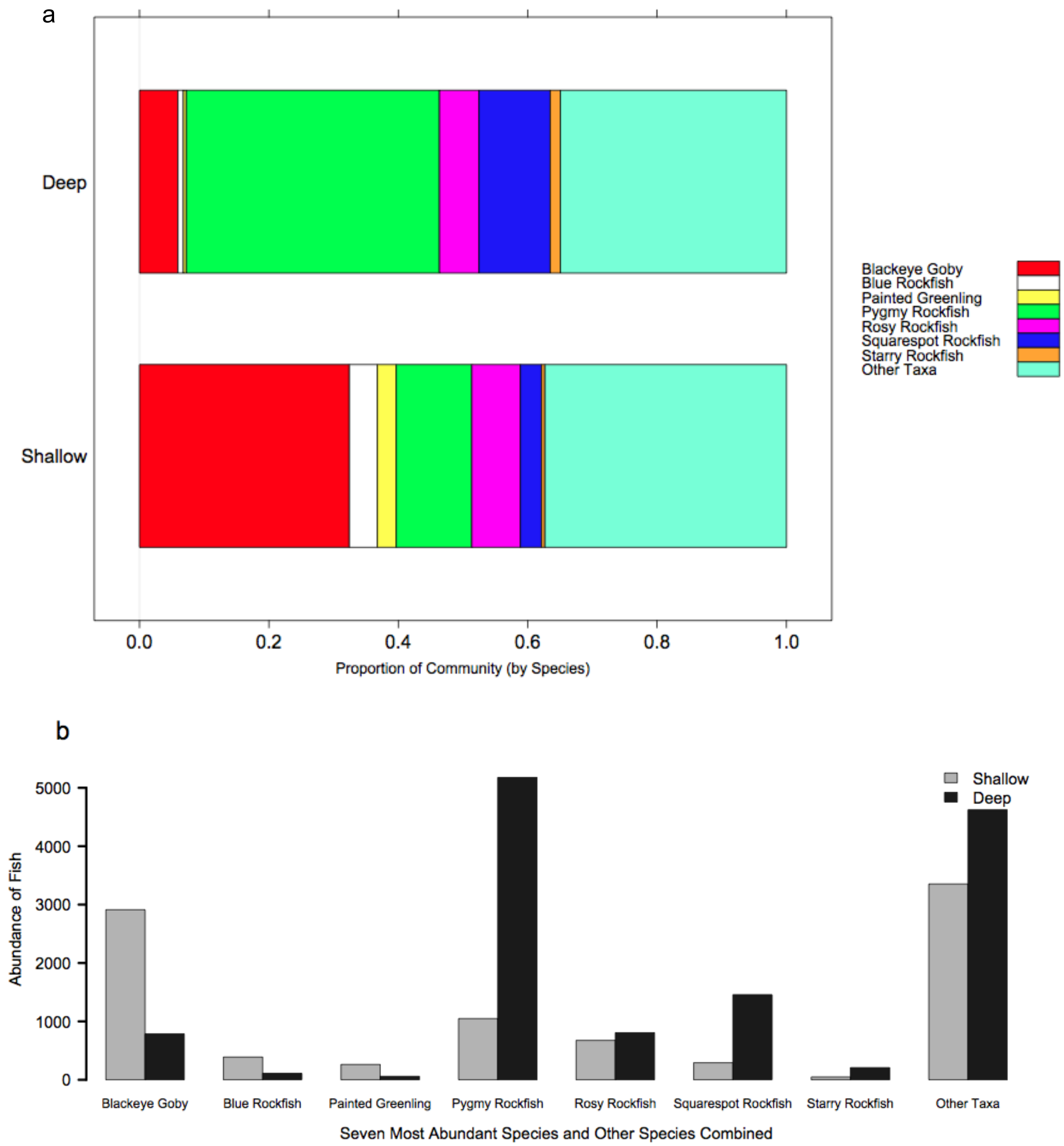


Fig. 5 Species composition of the seven most abundant species by depth category near Point Lobos. The assemblage composition in proportional abundance (a) and the observed abundance (b) are reported. The unidentified fishes, those not identified to the species level, and the 51 less-abundant species (whose abundance was less than 1% of the total abundance) are pooled into the "other" category. Depth classifications were defined as shallow (< 55 m) and deep (> 65 m)

Additionally, the density and biomass of all fishes significantly increased with increasing depth ($p = 0.001$, $p = 0.019$, respectively), whereas the evenness ($p = 0.019$) and heterogeneity ($p = 0.007$) significantly decreased with increasing depth (Table 3a, Appendix G). These significant relationships with depth were accounted for in subsequent analyses by comparing the regression residuals of depth and the biological response variable (density, biomass, evenness, or heterogeneity) with the subsequent independent habitat variable. There was no significant relationship between richness and depth; therefore, subsequent analyses used the original data for this biological response variable. After accounting for the effect of depth on the biological response variables at the assemblage level, there was no significant relationship among any of the biological response variables and rugosity (Appendix G).

Table 3 Assemblage, species-groups, and species-specific relationships with respect to depth and rugosity near Point Lobos. Results are grouped by analyses: assemblage indices with respect to depth and rugosity (a), species-group density and length distributions with respect to depth (b) and rugosity (c), and species-specific relationships with depth (d) and rugosity (e). Statistically significant relationships are in bold

a - Assemblage	**Depth**			**Rugosity**		
	p	**r^2**	**Direction**	**p**	**r^2**	**Direction**
Density (fish/10m^2)	**0.001**	0.419	**Positive**	0.811	0.003	No
Biomass (g/cm/10m^2)	**0.019**	0.224	**Positive**	0.552	0.016	No
Richness	0.408	0.031	No	0.142	0.095	Negative
Evenness	**0.019**	0.225	**Negative**	0.899	0.001	No
Heterogeneity	**0.007**	0.291	**Negative**	0.448	0.026	No

b - Species Groups (Depth)	**Density (fish/10m^2)**			**Length Distribution**		
	p	**r^2**	**Direction**	**p**	**D**	**Direction**
large rockfishes	**0.002**	0.354	**Positive**	0.993	0.130	No
dwarf rockfishes	**< 0.001**	0.670	**Positive**	**< 0.001**	0.215	**Positive**
large non-rockfishes	0.287	0.051	No	1.000	0.139	No
other benthic fishes	**< 0.001**	0.497	**Positive**	1.000	0.099	No

Table 3 cont.

c - Species Groups (Rugosity)	Density (fish/10m^2)			Length Distribution		
	p	r^2	Direction	p	D	Direction
large rockfishes	0.793	0.003	No	1.000	0.087	No
dwarf rockfishes	0.278	0.053	No			
Shallow				**< 0.001**	0.317	**Negative**
Deep				**< 0.001**	0.127	**Positive**
large non-rockfishes	0.688	0.007	No	1.000	0.139	No
other benthic fishes	**0.032**	0.192	**Positive**	1.000	0.035	No

d - Specific Species (Depth)	Density (fish/10m^2)			Biomass (g/cm/10m^2)		
	p	r^2	Direction	p	r^2	Direction
Blackeye Goby	**0.006**	0.295	**Negative**	**0.022**	0.215	**Negative**
Blue Rockfish	**0.047**	0.168	**Negative**	0.059	0.152	No
Painted Greenling	**< 0.001**	0.439	**Negative**	**0.001**	0.404	**Negative**
Pygmy Rockfish	**< 0.001**	0.533	**Positive**	**0.001**	0.418	**Positive**
Rosy Rockfish	**0.008**	0.278	**Positive**	**0.001**	0.428	**Positive**
Squarespot Rockfish	**0.001**	0.382	**Positive**	**< 0.001**	0.559	**Positive**
Starry Rockfish	**< 0.001**	0.539	**Positive**	**0.001**	0.419	**Positive**
	Mean Length (cm)			**Length Distribution**		
	p	r^2	Direction	p	D	Direction
Blackeye Goby	**0.045**	0.170	**Negative**	0.998	0.057	No
Blue Rockfish	0.063	0.148	No	0.282	0.324	No
Painted Greenling	**< 0.001**	0.694	**Negative**	0.999	0.167	No
Pygmy Rockfish	**< 0.001**	0.874	**Positive**	**< 0.001**	0.296	**Positive**
Rosy Rockfish	**0.001**	0.404	**Positive**	0.085	0.222	No
Squarespot Rockfish	**< 0.001**	0.720	**Positive**	0.248	0.207	No
Starry Rockfish	**0.024**	0.210	**Positive**	1.000	0.071	No

Table 3 cont.

e - Specific Species (Rugosity)	Density (fish/10m^2)			Biomass (g/cm/10m^2)		
	p	r^2	Direction	p	r^2	Direction
Blackeye Goby	0.459	0.025	No	0.460	0.025	No
Blue Rockfish	**0.023**	0.213	**Negative**	0.116	0.108	No
Painted Greenling	**0.014**	0.243	**Positive**	**0.013**	0.248	**Positive**
Pygmy Rockfish	0.242	0.062	No	**0.024**	0.212	**Positive**
Rosy Rockfish	0.589	0.014	No	0.718	0.006	No
Squarespot Rockfish	0.839	0.002	No	0.982	0.000	No
Starry Rockfish	0.661	0.009	No	0.817	0.002	No
	Mean Length (cm)			**Length Distribution**		
	p	**r^2**	**Direction**	**p**	**D**	**Direction**
Blackeye Goby	0.947	0.000	No	0.994	0.048	No
Blue Rockfish	0.057	0.155	No	0.807	0.205	No
Painted Greenling	**0.033**	0.191	**Positive**	0.998	0.145	No
Pygmy Rockfish						
Shallow	0.994	0.000	No	**< 0.001**	0.749	**Positive**
Deep	0.136	0.098	No	**< 0.001**	0.147	**Positive**
Rosy Rockfish	0.243	0.061	No	1.000	0.030	No
Squarespot Rockfish	0.118	0.107	No	0.347	0.157	No
Starry Rockfish	0.927	0.417	No	0.996	0.167	No

Proximity to Edge. Total density of fishes was not significantly different between the edge and interior zones in shallow rocky bank patches ($p = 0.627$; Fig. 6a, Table 4). Although the mean density of fishes in deep rocky bank patches was somewhat greater in the edge than in the interior, it was not significantly different ($p = 0.099$; Fig. 6a). The fish assemblage biomass did not differ between the edge and interior zones in shallow rocky bank patches ($p = 0.463$; Table 4), but was significantly greater in the edge than the interior zones in deep patches ($p = 0.036$).

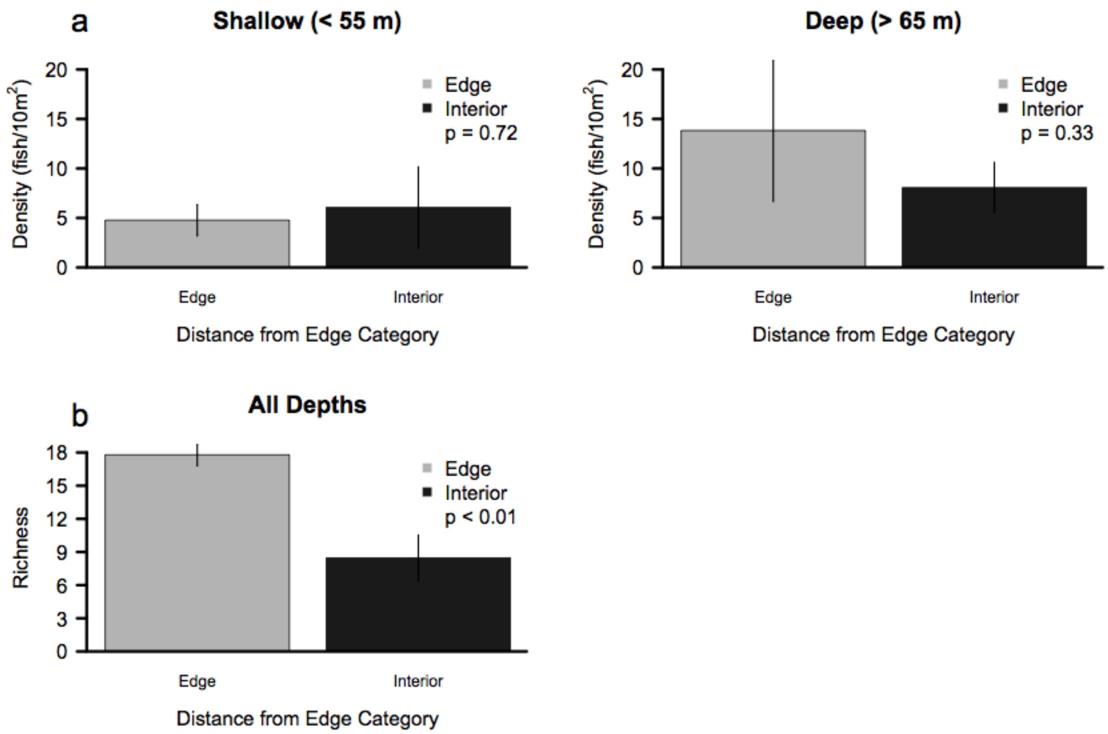


Fig. 6 Comparison of assemblage biological response variables (density and species richness) with respect to distance from rocky bank patch edge near Point Lobos. The results are of the density (a) and species richness (b). If the assemblage index was significantly correlated with depth, the analysis was run with binned data. Gray denotes the edge zone and black denotes the interior zone. Standard error is plotted as vertical bars. P-values are included in the legends

Table 4 Assemblage biological response variables (density, biomass, richness, evenness, and heterogeneity) with respect to distance from rocky bank patch edge near Point Lobos. If the assemblage index was significantly correlated with depth, the analysis was run with binned data. Statistically significant relationships are in bold

	Shallow or Pooled				Deep			
	p	**df**	**F-ratio**	**Direction**	**p**	**df**	**F-ratio**	**Direction**
Density (fish/10m^2)	0.627	2	0.242	No	0.099	2	3.000	No
Biomass (g/cm/10m^2)	0.463	2	0.555	No	0.036	2	5.058	Edge
Richness	**< 0.001**	2	14.904	**Edge**				
Evenness	**0.008**	2	8.484	**Edge**	**0.026**	2	5.786	**Edge**
Heterogeneity	**0.027**	2	5.584	**Edge**	**0.007**	2	9.043	**Edge**

The number of observed species was significantly greater in the edge than the interior zones near Point Lobos ($p < 0.001$; Fig. 6b). Similarly, evenness was significantly greater in the edge than the interior zones in both shallow ($p = 0.008$) and deep ($p = 0.026$) sections near Point Lobos (Table 4), meaning there were fewer dominant species in the assemblage at the edge of rocky bank patches than in the interior. Therefore, heterogeneity also was significantly greater in the edge than the interior zones across the depth range ($p = 0.008$, $p = 0.026$; Table 4). The species composition between the edge and interior zones in shallow patches was 0.713 similar, but only 0.424 similar in deep patches (Fig. 7). This indicates a difference in edge effects of assemblage diversity between the shallow and deep patches similar to those observed in the density and biomass results.

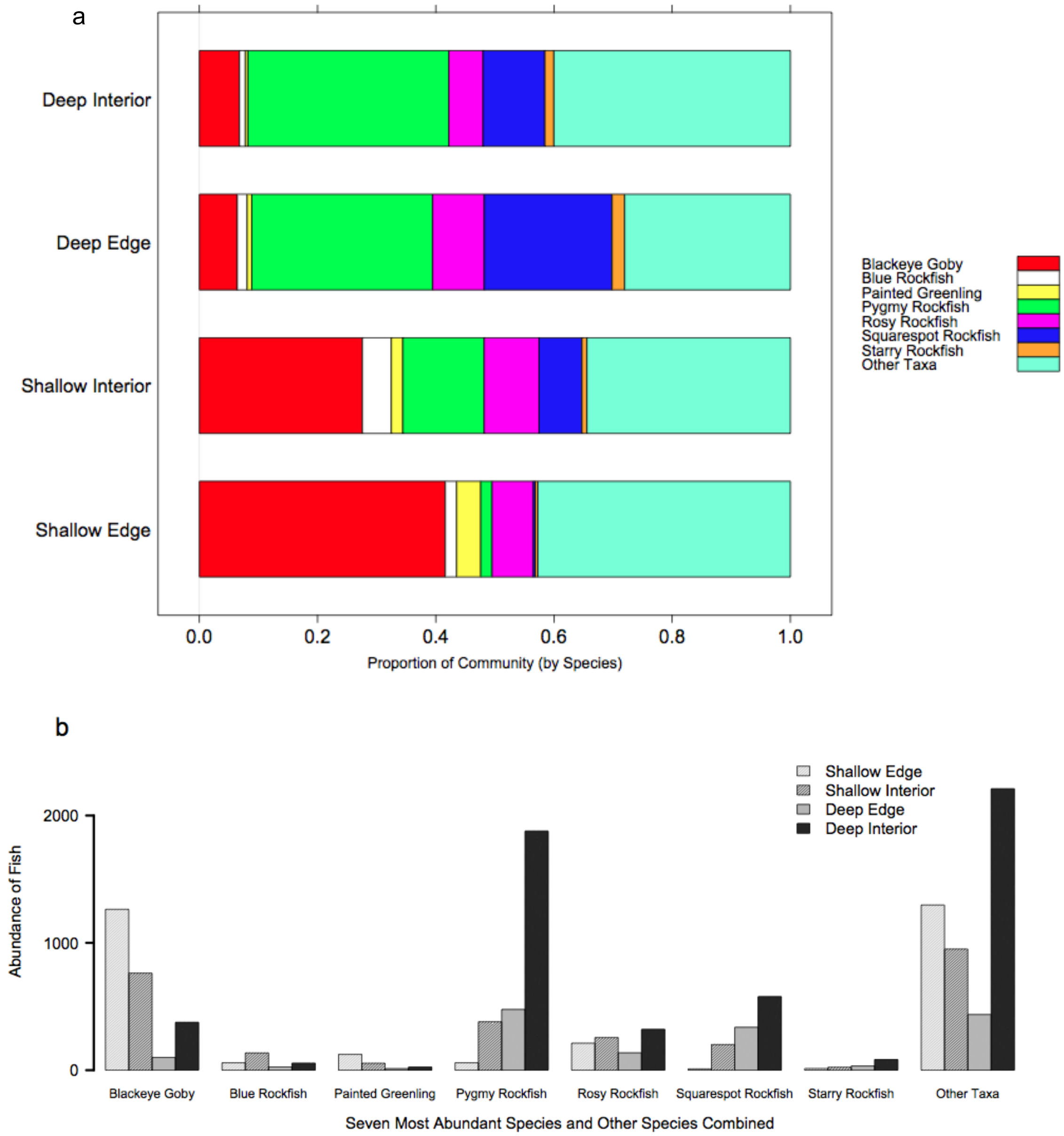


Fig. 7 Species composition of the seven most abundant species by depth category and proximity to edge near Point Lobos. The assemblage composition in proportional abundance (a) and the observed abundance (b) are reported. The unidentified fishes, those not identified to the species level, and the 51 less-abundant species (whose abundance was less than 1% of the total abundance) are pooled into the “other” category. Depth classifications were defined as shallow (< 55 m) and deep (> 65 m)

Patch Shape (P:A Ratio). Neither the density nor biomass of all fishes combined was significantly correlated with the P:A ratio (p = 0.559 and p = 0.192 respectively; Table 5, Fig. 8a). However, there was a significant negative relationship between richness and rocky bank patch shape (p = 0.012; Fig. 8b). Fewer species were observed in rocky bank patches with more complex boundaries. In fact, rocky bank patch shape explained 25.4% of the variability in richness in the nearshore fish assemblage. However, there was no significant relationship between assemblage evenness or heterogeneity and P:A ratio (p = 0.362, p = 0.742).

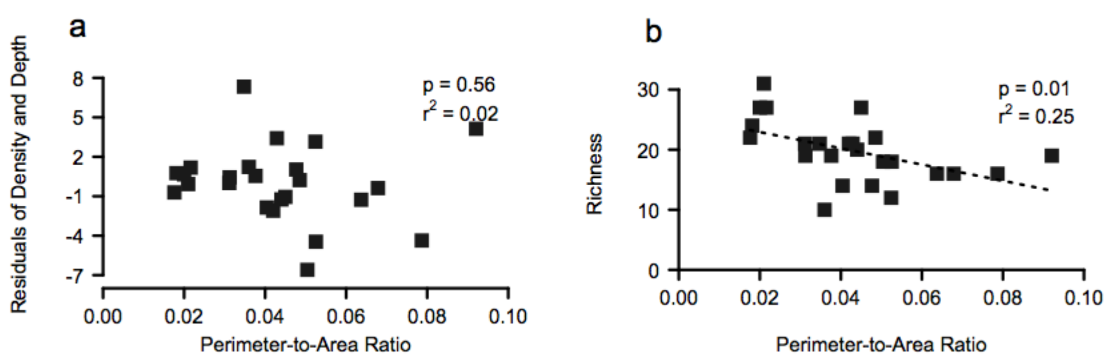


Fig. 8 Comparison of assemblage biological response variables (density and richness) with respect to patch shape of rocky bank patches near Point Lobos. Results are of the density (a) and richness (b). If the assemblage index was significantly correlated with depth, the analysis was run against the residuals data. Significant relationships are denoted by a dotted regression line. P-values and r^2 values are included in the legends

Table 5 Assemblage biological response variables (density, biomass, richness, evenness, and heterogeneity) with respect to patch shape of rocky bank patches near Point Lobos. If the assemblage index was significantly correlated with depth, the analysis was run against the residuals data. Statistically significant relationships are in bold

	p	r^2	Direction
Density (fish/10m^2)	0.559	0.016	No
Biomass (g/cm/10m^2)	0.192	0.076	No
Richness	**0.012**	0.254	**Negative**
Evenness	0.362	0.038	No
Heterogeneity	0.742	0.005	No

Patch Size (Area). Neither the density nor biomass of all fishes was significantly correlated with rocky bank patch size (p = 0.483, p = 0.064; Fig. 9a, Table 6). However, there was a significant positive relationship between richness and area (p < 0.001; Fig. 9b). In fact, rocky bank patch size explained 48.2% of the variability in species richness. But there was no relationship between the dominance of species within the assemblage or the overall diversity and area (p = 0.895, p = 0.082, Table 6).

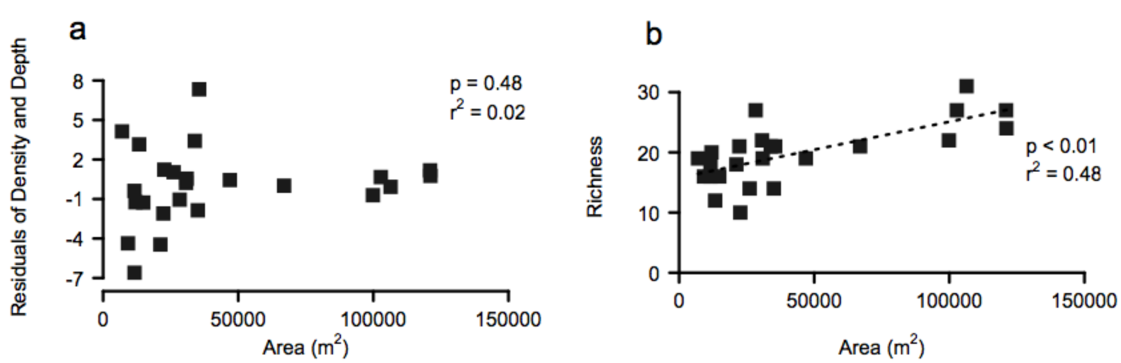


Fig. 9 Comparison of assemblage biological response variables (density and richness) with respect to patch size of rocky bank patches near Point Lobos. Results are of the density (a) and richness (b). If the assemblage index was significantly correlated with depth, the analysis was run against the residuals data. Significant relationships are denoted by a dotted regression line. P-values and r^2 values are included in the legends

Table 6 Assemblage biological response variables (density, biomass, richness, evenness, and heterogeneity) with respect to patch size of rocky bank patches near Point Lobos. If the assemblage index was significantly correlated with depth, the analysis was run against the residuals data. Statistically significant relationships are in bold

	p	r^2	Direction
Density (fish/10m^2)	0.483	0.023	No
Biomass (g/cm/10m^2)	0.064	0.147	No
Richness	**< 0.001**	0.482	**Positive**
Evenness	0.895	0.001	No
Heterogeneity	0.082	0.131	No

Species Group Analyses

Depth and Rugosity. The density and length distribution of the four species groups varied with respect to depth. The density of large rockfishes, dwarf rockfishes, and other benthic fishes significantly increased with increasing depth ($p = 0.002$, $p < 0.001$, $p < 0.001$ respectively; Table 3b, Appendix F). Additionally, the length distribution of dwarf rockfishes increased significantly with depth ($p < 0.001$). These significant relationships with depth for the density and length distributions of different species groups were accounted for in subsequent analyses by using the regression residuals of depth and the biological response variable for the appropriate species group (i.e., density of large rockfishes, dwarf rockfishes, and other benthic fishes) and by binning the length distribution data by depth categories for dwarf rockfishes. There were no significant relationships among the remaining species groups' density or length distributions with respect to depth, therefore subsequent analyses used the original data for these two biological response variables.

Although the assemblage indices did not correlate with rugosity, there were significant relationships between rugosity and some of the species groups' density and length distributions (Table 3c, Appendix F). For example, the density of other benthic fishes was positively correlated with rugosity ($p = 0.032$). In addition, the length distribution of dwarf rockfishes significantly decreased with increasing rugosity ($p = 0.004$). The density and length distribution for the other species groups did not significantly vary with changes in rugosity; therefore, the original, or depth-adjusted, data were used for further analyses with the remaining independent habitat variables.

Proximity to Edge. As expected, positive edge effects were observed in some of the assemblage indices investigated (e.g., diversity indices and biomass, see above). Therefore, this study investigated if these trends of the assemblage structure could be explained by patterns of the four species groups. The relative abundance of each species group was proportionally distributed between the edge and interior zones of rocky bank patches. This means that the observed abundance in the edge and interior zones did not differ from the expected abundance based on the available area of the edge and interior zones (Appendix G). However, differences in densities were detected between the edge and interior zones (Table 7). For example, the density of large rockfishes and other benthic fishes were both significantly greater in the edge zone as compared to the interior zones ($p = 0.046$, $p = 0.013$; Fig. 10a). The densities of the dwarf rockfishes and large non-rockfishes were not significantly different ($p > 0.05$) with respect to proximity to the edge for either shallow or deep rocky bank patches.

Table 7 Biological response variables (density and length distributions) of the species groups with respect to distance from the rocky bank patch edge near Point Lobos. The results are for the density (a) and the length distributions (b). If the species-group index was significantly correlated with depth, the analysis was run with binned data. Statistically significant relationships are in bold

a - Density (fish/10m^2)	Shallow				Deep			
	p	df	F-ratio	Direction	p	df	F-ratio	Direction
large rockfishes	0.286	2	1.19	Edge	**0.046**	2	4.547	**Edge**
dwarf rockfishes	0.383	2	0.788	Core	0.550	2	0.369	Edge
large non-rockfishes	0.511	2	0.438	Edge				
other benthic fishes	**0.013**	2	7.216	**Edge**	0.552	2	0.365	No

b - Length Distribution	p	D	Direction
large rockfishes	0.574	0.244	No
dwarf rockfishes	**< 0.001**	0.787	**Core**
	0.021	0.286	**Edge**
large non-rockfishes	0.574	0.244	No
other benthic fishes	0.964	0.167	No

The length distribution of dwarf rockfishes was significantly different between the edge and interior zones. In shallow rocky bank patches, longer dwarf rockfishes were observed in the interior zone ($p < 0.001$; Fig. 10b). Whereas in deep rocky bank patches, dwarf rockfishes of longer lengths were observed in the edge zone rather than the interior zone ($p = 0.021$; Fig. 10b). There was no relationship among the length distribution of large rockfishes, large non-rockfishes, or other benthic fishes and the proximity to the edge for either shallow or deep rocky bank patches (Table 7).

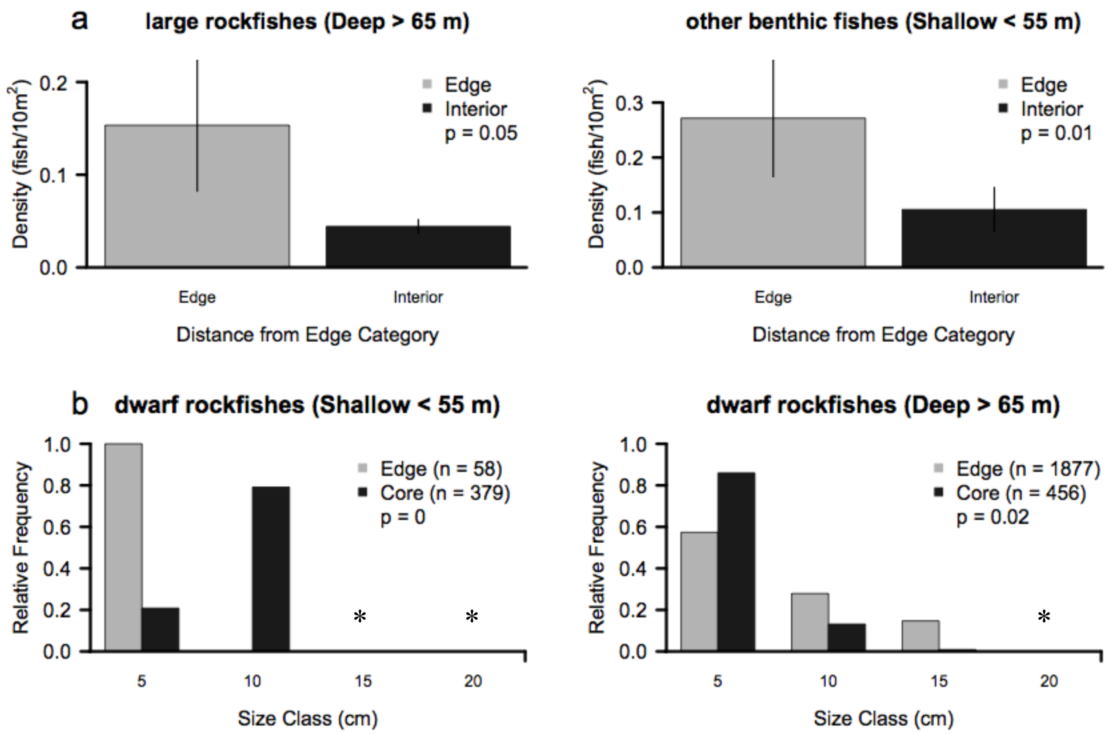


Fig. 10 Comparison of biological response variables (density and length distributions) of species groups with respect to distance from the rocky bank patch edge near Point Lobos. A is the density of large rockfishes and other benthic fishes; b is the length distributions of dwarf rockfishes in shallow and deep rocky bank patches. If the species-group index was significantly correlated with depth, the analysis was run with binned data. Gray denotes the edge zone and black denotes the interior zone. Asterisks indicate size classes in which fish were observed in abundances too small to be observed on the relative frequency histograms. Standard error is plotted as vertical bars. P-values are included in the legends

Patch Shape (P:A Ratio). Rocky bank patch shape displayed a significant correlation with the number of species within the nearshore fish assemblage. These results are opposite of what the edge results for the assemblage demonstrated. The relationship between patch shape and the fish assemblage may be species-specific, and thus patterns between the four species groups and patch shape were investigated.

Similar to the assemblage results, there was no significant relationship between the density of each species group and the P:A ratio (Table 8). Whereas three of the species groups were not significantly correlated with the P:A ratio, individuals of dwarf rockfishes were longer in rocky bank patches with greater P:A ratios in both shallow and deep rocky bank patches ($p = 0.001$ and $p < 0.001$ respectively; Table 8). Additionally, the goodness-of-fit results indicated that while the abundances of three of the four species groups were proportionally distributed between rocky bank patches of greater and lesser P:A ratios, the abundances of dwarf rockfishes were not evenly distributed between rocky bank patches of different P:A ratios (Appendix G). Instead, the observed abundance of dwarf rockfishes was greater than expected in patches of greater P:A ratios based on the available area in the rocky bank patches ($x^2 = 6.247$, $p = 0.012$; Appendix G).

Table 8 Biological response variables (density and length distributions) of the species groups with respect to patch shape of rocky bank patches near Point Lobos. If the species-group index was significantly correlated with depth, the analysis was run against the residuals or the binned data. Statistically significant relationships are in bold

	Density (fish/10m^2)			Length Distribution		
	p	**r^2**	**Direction**	**p**	**D**	**Direction**
large rockfishes	0.923	0.000	No	0.681	0.220	Negative
dwarf rockfishes	0.130	0.101	No	**0.001**	0.346	**Positive**
				< 0.001	0.214	**Positive**
large non-rockfishes	0.961	0.000	No	0.889	0.300	No
other benthic fishes	0.901	0.001	No	0.999	0.110	No

Patch Size (Area). To determine if the patterns of the assemblage with respect to patch size were driven by species groups within the assemblage, the relationship of the density and length distributions of the species groups was examined with respect to area.

However, there was no significant relationship between the density of any species group and patch area (Table 9). Similar to the patch shape results, dwarf rockfishes was the only species group in which a significant relationship between the length distribution and patch area was observed. Dwarf rockfishes were significantly longer in rocky bank patches of greater area for both shallow and deep rocky bank patches ($p = 0.001$ and $p < 0.001$ respectively; Table 9).

Table 9 Biological response variables (density and length distributions) of the species groups with respect to patch size of rocky bank patches near Point Lobos. If the species-group index was significantly correlated with depth, the analysis was run against the residuals or the binned data. Statistically significant relationships are in bold

	Density (fish/10m^2)			**Length Distribution**		
	p	**r^2**	**Direction**	**p**	**D**	**Direction**
large rockfishes	0.398	0.033	No	0.990	0.131	No
dwarf rockfishes	0.053	0.159	Positive	**0.001**	0.351	**Negative**
				< 0.001	0.222	**Positive**
large non-rockfishes	0.412	0.031	No	1.000	0.139	No
other benthic fishes	0.539	0.017	No	0.995	0.118	No

The abundance of the different species groups varied between rocky bank patches of lesser and greater area. The abundances of two of the four species groups (dwarf rockfishes and other benthic fishes) were not proportionally distributed between patches of lesser and greater area. Instead the observed abundances of dwarf rockfishes was greater than expected in patches of lesser area ($x^2 = 12.914$, $p < 0.001$), whereas the observed abundance of other benthic fishes was greater in patches of greater area based on the available area in the rocky bank patches ($x^2 = 6.465$, $p = 0.011$; Appendix G). This indicated that the size of a rocky bank patch affected the relative abundances of these species groups.

Species-Specific Analyses

Depth and Rugosity. The density of all of the seven most abundant species varied with respect to depth (Table 3d, Appendix F). The density of Blackeye Goby ($p = 0.006$), Blue Rockfish ($p = 0.047$), and Painted Greenling ($p < 0.001$) significantly decreased with increasing depth, whereas the density of Pygmy ($p < 0.001$), Rosy ($p = 0.008$), Squarespot ($p = 0.001$), and Starry Rockfish ($p < 0.001$) significantly increased with increasing depth. Patterns in fish biomass were the same as those observed for species-specific density, except there was no significant difference in biomass of Blue Rockfish with depth (Table 3d, Appendix F). The biomass of Blackeye Goby ($p = 0.022$) and Painted Greenling ($p = 0.001$) significantly decreased with increasing depth, whereas the biomass of Pygmy ($p = 0.001$), Rosy ($p = 0.001$), Squarespot ($p < 0.001$), and Starry Rockfish ($p = 0.001$) significantly increased with increasing depth.

As expected, the patterns in mean length for all seven species were the same as those observed for biomass for each species (Table 3d, Appendix F). The mean length of Blackeye Goby ($p = 0.045$) and Painted Greenling ($p < 0.001$) significantly decreased with increasing depth, whereas the mean length of Pygmy ($p < 0.001$), Rosy ($p = 0.001$), Squarespot ($p < 0.001$), and Starry Rockfish ($p = 0.024$) significantly increased with increasing depth. Pygmy rockfish, however, was the only species whose length frequency distribution significantly varied with depth (Table 3d, Appendix F). Pygmy Rockfish of longer size were observed in deeper rocky bank patches ($p < 0.001$).

Whenever a biological response variable was significantly correlated with depth, the data were either split into shallow and deep depth bins (length frequency distribution) or the regression residuals of depth and the biological response variable (density, biomass, and mean length) was used for the subsequent analyses. When the species-specific biological response variables did not significantly correlate with depth (e.g., Blue Rockfish biomass) the original data was used to analyze patterns with respect to other independent habitat variables.

Similar to the relationships between species groups and rugosity, there were significant relationships between rugosity and biological response variables for some of the seven most abundant species (Table 3e, Appendix F). For example, the density of Blue Rockfish was negatively correlated with rugosity ($p = 0.023$), whereas the density of Painted Greenling was positively correlated ($p = 0.014$). There was no significant difference in the density of the remaining species with respect to rugosity. There was a significant increase in the biomass of both Painted Greenling ($p = 0.013$) and Pygmy Rockfish ($p = 0.024$) with increasing rugosity (Table 3e, Appendix G), but no significant relationship for biomass of the other five species. Also, significant changes in the lengths of Painted Greenling and Pygmy Rockfish were observed (Table 3e, Appendix F). The mean length of Painted Greenling was significantly longer in rocky bank patches with greater rugosity ($p = 0.033$). Although the mean length for Pygmy Rockfish was similar with respect to rugosity, the length frequency distributions significantly differed in both shallow and deep patches ($p < 0.001$, $p < 0.001$).

Proximity to Edge. Knowing that the species groups responded differently to the edge and interior zones of rocky bank patches, whether the seven most abundant species also varied with respect to the edge of a rocky bank patch was investigated. Blackeye Goby, which was not included in any of the species groups, was the only species whose density and size correlated with the edge or interior zone (Table 10). The density ($p = 0.046$) and biomass ($p = 0.001$) of the Blackeye Goby were significantly greater in the edge zone than the interior zone in deep patches (Fig. 11a-b). The mean lengths of Blackeye Goby ($p = 0.021$, $p = 0.003$; Fig. 11c) and Rosy Rockfish ($p = 0.031$, $p = 0.005$; Fig. 11e) were significantly longer in the edge zone in both shallow and deep patches. Additionally, the mean lengths of Pygmy ($p = 0.002$; Fig. 11d), Squarespot ($p = 0.003$; Fig. 11f), and Starry Rockfishes ($p = 0.014$; Fig. 11g) also were significantly longer in the edge zone of the rocky bank patch, but only in deep patches. There was no relationship among density, biomass, mean length, or length frequency distributions for either Blue Rockfish or Painted Greenling with respect to proximity to rocky bank patch edge (Table 10).

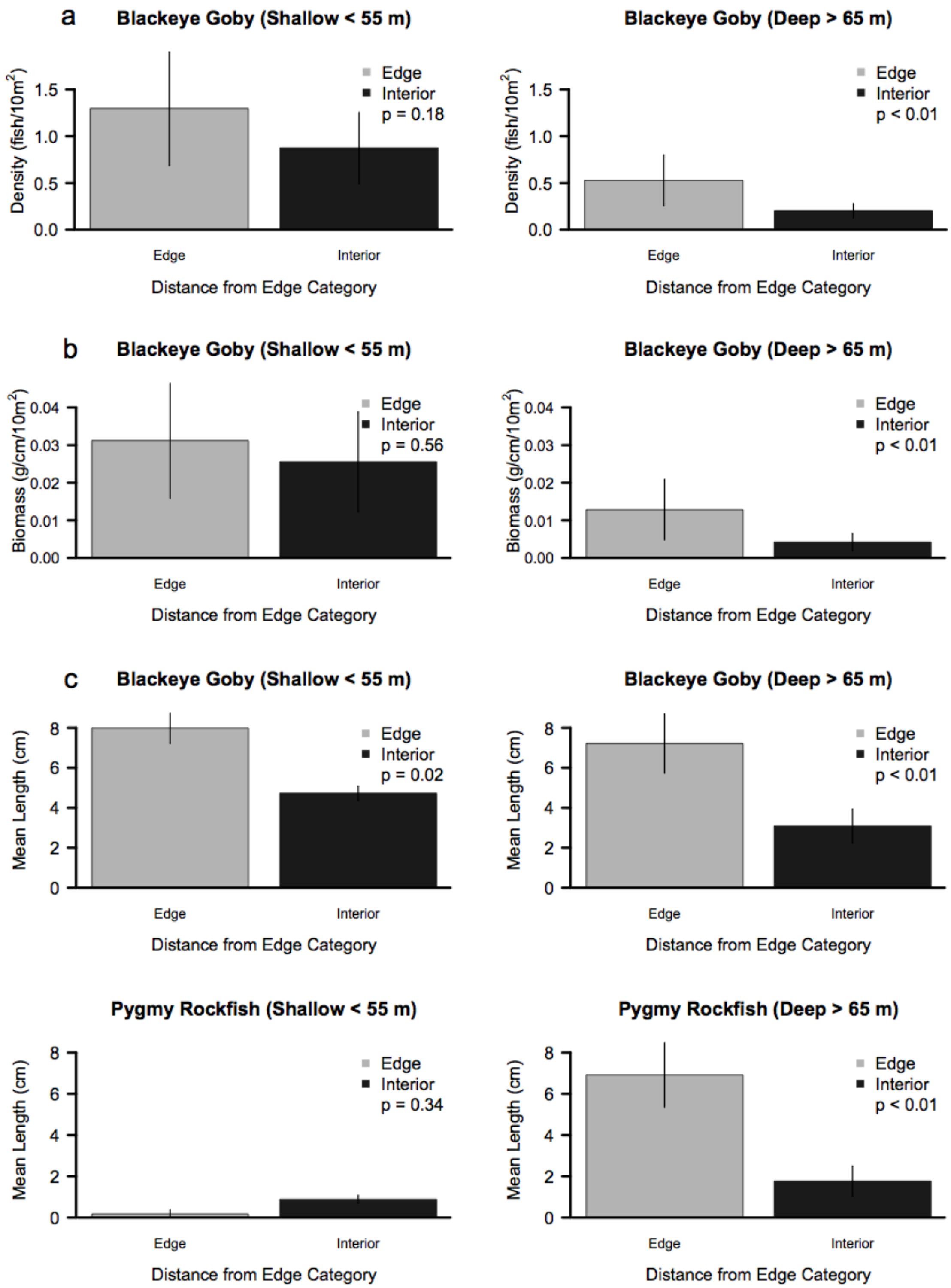
Table 10 Biological response variables (density, biomass, mean length, and length distributions) of the specific species with respect to distance from rocky bank patch edge near Point Lobos. The results are for density (a), biomass (b), mean length (c), and length distributions (d). If the species-group index was significantly correlated with depth, the analysis was run against the residuals or binned data. Statistically significant relationships are in bold

a - Density (fish/10m^2)	**Shallow**				**Deep**			
	p	**df**	**F-ratio**	**Direction**	**p**	**df**	**F-ratio**	**Direction**
Blackeye Goby	0.182	2	1.886	Edge	**0.007**	2	8.953	**Edge**
Blue Rockfish	0.827	2	0.049	Edge	0.312	2	1.076	Edge
Painted Greenling	0.074	2	3.492	Edge	0.543	2	0.382	Edge
Pygmy Rockfish	0.389	2	0.770	Core	0.188	2	1.860	Edge
Rosy Rockfish	0.913	2	0.012	No	0.063	2	3.889	Edge
Squarespot Rockfish	0.533	2	0.401	Core	0.600	2	0.283	Core
Starry Rockfish	0.627	2	0.242	No	0.099	2	3.000	Edge

b - Biomass (g/cm/10m^2)	**Shallow**				**Deep**			
	p	**df**	**F-ratio**	**Direction**	**p**	**df**	**F-ratio**	**Direction**
Blackeye Goby	0.563	2	0.345	Edge	**0.001**	2	14.142	**Edge**
Blue Rockfish	0.553	2	0.358	Edge				
Painted Greenling	0.238	2	1.466	Edge	0.515	2	0.440	Edge
Pygmy Rockfish	0.340	2	0.949	Core	0.093	2	3.129	Edge
Rosy Rockfish	0.594	2	0.291	No	0.116	2	2.703	Edge
Squarespot Rockfish	0.491	2	0.489	Core	0.191	2	1.831	Edge
Starry Rockfish	0.672	2	0.184	Core	0.307	2	1.098	Edge

c - Mean Length (cm)	**Shallow**				**Deep**			
	p	**df**	**F-ratio**	**Direction**	**p**	**df**	**F-ratio**	**Direction**
Blackeye Goby	**0.021**	2	6.073	**Edge**	**0.003**	2	11.015	**Edge**
Blue Rockfish	0.058	2	3.750	No				
Painted Greenling	0.166	2	2.042	No	0.462	2	0.561	No
Pygmy Rockfish	0.337	2	0.961	No	**0.002**	2	13.146	**Edge**
Rosy Rockfish	**0.031**	2	5.245	**Edge**	**0.005**	2	10.143	**Edge**
Squarespot Rockfish	0.790	2	0.073	No	**0.003**	2	11.703	**Edge**
Starry Rockfish	0.833	2	0.045	No	**0.014**	2	7.298	**Edge**

d - Length Distribution	**Shallow**			**Deep**		
	p	**D**	**Direction**	**p**	**D**	**Direction**
Blackeye Goby	1.000	0.031	No			
Blue Rockfish	1.000	0.125	No			
Painted Greenling	1.000	0.045	No			
Pygmy Rockfish	1.000	0.100	No	1.000	0.000	No
Rosy Rockfish	1.000	0.200	No			
Squarespot Rockfish	1.000	0.171	No			
Starry Rockfish	0.999	0.400	No			


a
Blackeye Goby (Shallow < 55 m)
Density (fish/10m²)
Edge
Interior
p = 0.18
Distance from Edge Category
Blackeye Goby (Deep > 65 m)
p < 0.01
b
Biomass (g/cm/10m²)
p = 0.56
c
Mean Length (cm)
p = 0.02
Pygmy Rockfish (Shallow < 55 m)
p = 0.34
Pygmy Rockfish (Deep > 65 m)

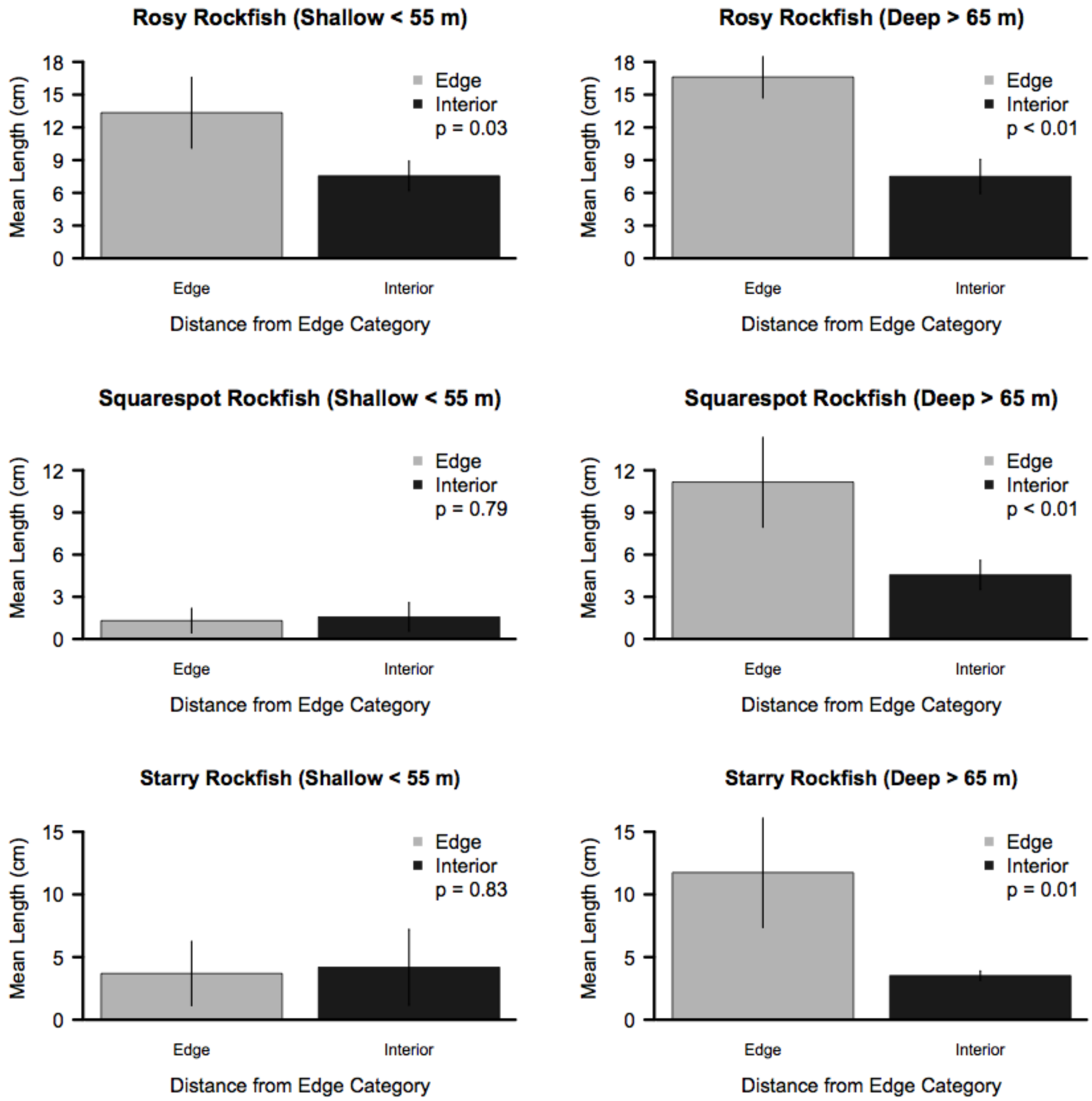


Fig. 11 Comparison of biological response variables (density, biomass, and mean length) of specific species with respect to distance from rocky bank patch edge near Point Lobos. A is the density and b is the biomass of Blackeye Goby. The mean length of Blackeye Goby as well as Pygmy, Rosy, Squarespot, and Starry Rockfish (c) are also reported. If the species index was significantly correlated with depth, the analysis was run with binned data. Gray denotes the edge zone and black denotes the interior zone. Standard error is plotted as vertical bars. P-values are included in the legends

Patch Shape (P:A Ratio). Results from the four species groups did not further explain the relationship between assemblage biological response variables and patch shape. However, significant patterns among species-specific biological response variables and P:A ratio were observed. These patterns, especially those observed in length frequency distributions, could be driving the assemblage response of length frequencies to patch shape. For example, the length frequency distributions of Pygmy and Squarespot Rockfish were significantly different between patches with lesser and greater P:A ratios, respectively ($p < 0.001$, $p = 0.045$; Fig. 12a-b). For both of these species, individuals in patches with more complex shapes (greater P:A ratio) had longer mean lengths than patches with less complex shapes (lesser P:A ratio). The relationship between Pygmy Rockfish and patch shape was only significant for deep patches because none were observed in shallow patches of high P:A ratio near Point Lobos (Fig. 12a). However, the density, biomass, and mean length of Pygmy and Squarespot Rockfish did not vary significantly with respect to patch shape (Table 11). Additionally, none of the other five species demonstrated significant patterns with respect to P:A ratio for density, biomass, mean length, or length frequency distributions (Table 8).

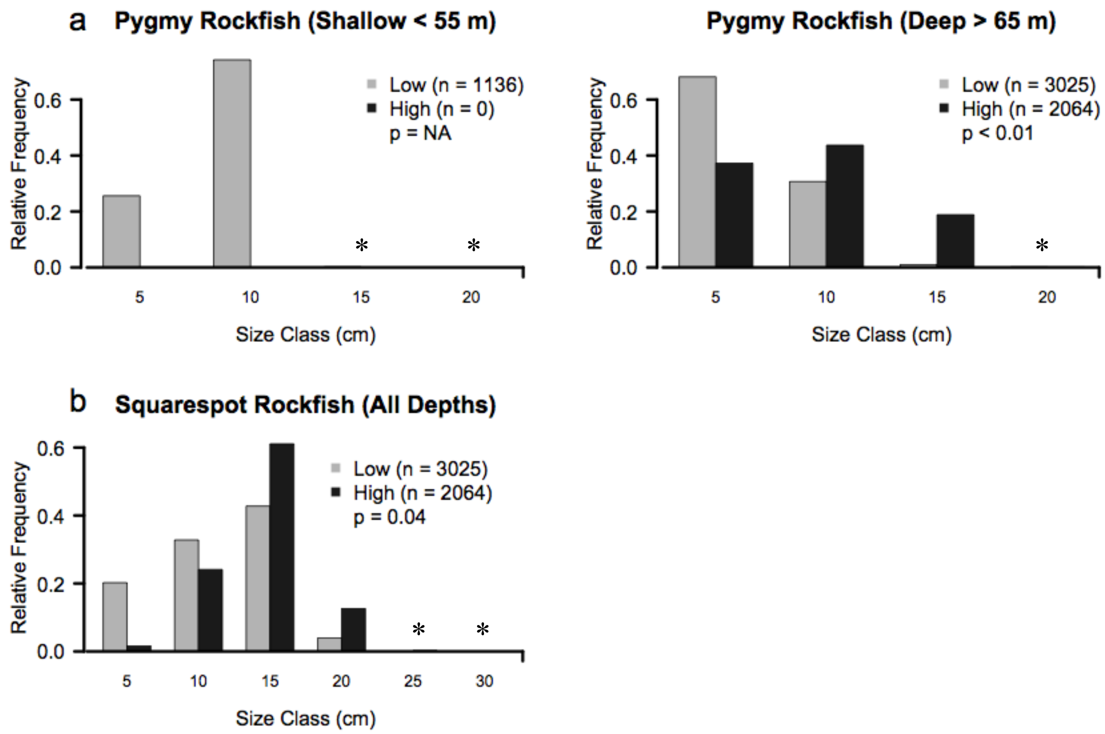


Fig. 12 Comparison of biological response variables (length distributions) of specific species with respect to patch shape of rocky bank patches near Point Lobos. Results are for Pygmy (a) and Squarespot Rockfish (b). If the species index was significantly correlated with depth, the analysis was run with binned data. Gray denotes the low perimeter-to-area ratio category and black denotes the high perimeter-to-area ratio category. Asterisks indicate size classes in which fish were observed in abundances too small to be observed on the relative frequency histograms. P-values are included in the legends; NA means that statistical tests were not possible due to lack of data in a category

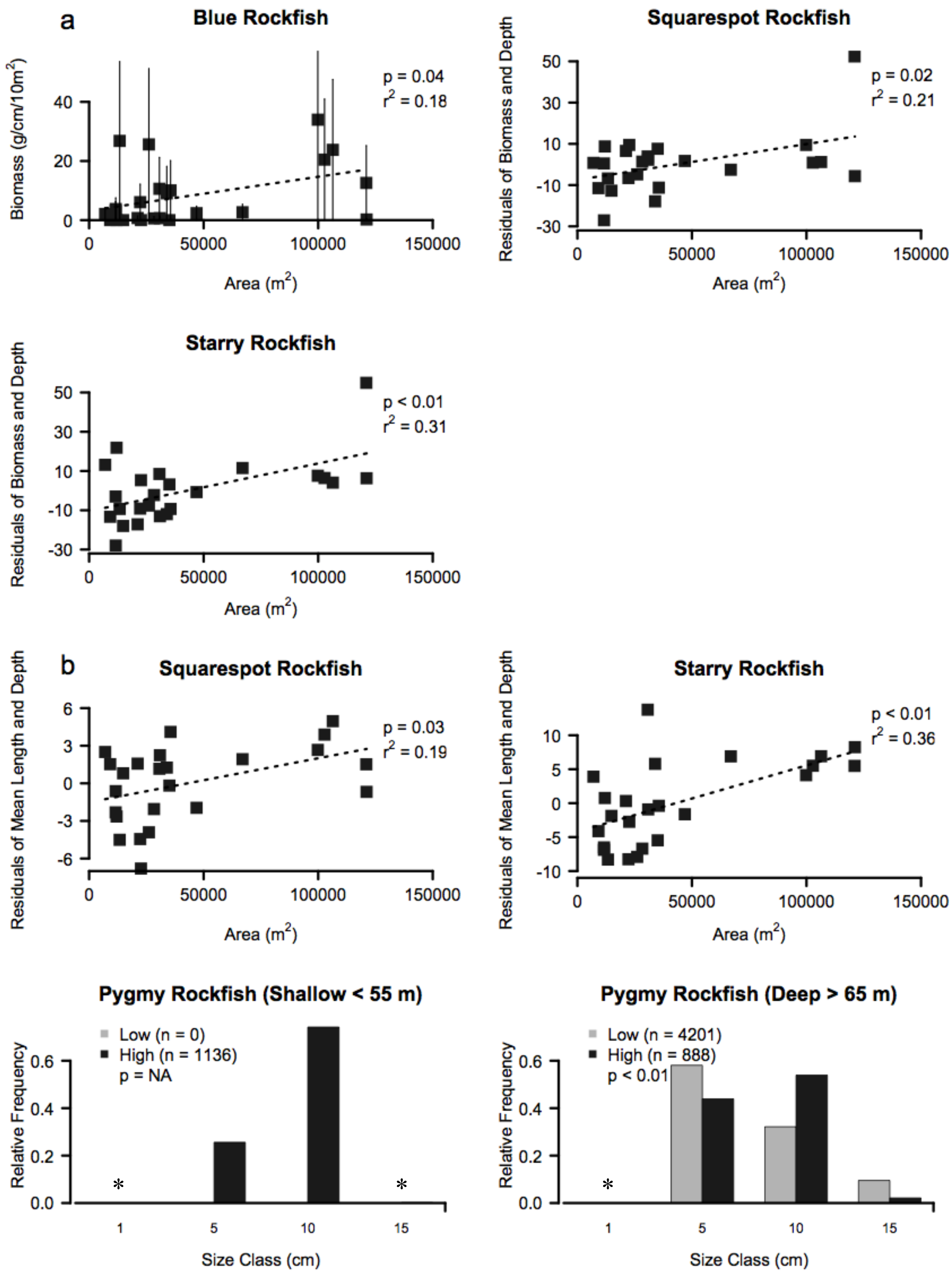
Table 11 Biological response variables (density, biomass, mean length, and length distributions) of the specific species with respect to patch shape of rocky bank patches near Point Lobos. The results are for density, biomass, mean length, and length distributions. If the species-specific index was significantly correlated with depth, the analysis was run against the residuals or with binned data. Statistically significant relationships are in bold; N/A denotes analyses that could not be tested due to insufficient data

	Density (fish/10m^2)			Biomass (g/cm/10m^2)		
	p	**r^2**	**Direction**	**p**	**r^2**	**Direction**
Blackeye Goby	0.414	0.031	No	0.471	0.024	No
Blue Rockfish	0.387	0.034	No	0.071	0.140	Negative
Painted Greenling	0.879	0.001	No	0.579	0.014	No
Pygmy Rockfish	0.591	0.013	No	0.341	0.041	No
Rosy Rockfish	0.160	0.088	No	0.118	0.107	No
Squarespot Rockfish	0.075	0.137	Negative	0.113	0.110	No
Starry Rockfish	0.734	0.005	No	0.097	0.120	No
	Mean Length (cm)			**Length Distribution**		
	p	**r^2**	**Direction**	**p**	**D**	**Direction**
Blackeye Goby	0.621	0.011	No	1.000	0.009	No
Blue Rockfish	0.325	0.044	No	1.000	0.108	No
Painted Greenling	0.161	0.087	No	1.000	0.114	No
Pygmy Rockfish	0.672	0.008	No			
Shallow				N/A	N/A	N/A
Deep				**< 0.001**	0.308	**Positive**
Rosy Rockfish	0.647	0.010	No	1.000	0.053	No
Squarespot Rockfish	0.503	0.021	No	**0.035**	0.273	**Positive**
Starry Rockfish	0.078	0.134	No	0.845	0.252	No

Patch Size (Area). Similar to the species groups, there was no significant relationship between the species-specific density and area (Table 12). However, there was a positive relationship between patch area and the biomass of Blue, Squarespot, and Starry Rockfish ($p = 0.041$, $p = 0.025$, and $p = 0.005$, respectively; Fig. 13). As the patch size increased, the biomass of each of the observed species increased. There was a significant relationship between the patch area and mean length of Squarespot and Starry Rockfish ($p = 0.033$, $p = 0.002$; Fig. 13). Not only did the mean length of Squarespot Rockfish increase with patch size, but the length frequency distributions also were significantly different between patches with longer fishes observed in higher frequencies in patches of greater area ($p = 0.027$; Fig. 13). The length frequency distribution of the Pygmy Rockfish population also varied with respect to patch size ($p < 0.001$; Fig. 13). For both of these species, patches of greater area had increased proportions of longer individuals. These patterns aligned with the positive relationship between length frequencies of the dwarf rockfish species group and patch area.

Table 12 Biological response variables (density, biomass, mean length, and length distributions) of the specific species with respect to patch size of rocky bank patches near Point Lobos. The results are for density, biomass, mean length, and length distributions. If the species-specific index was significantly correlated with depth, the analysis was run against the residuals or with binned data. Statistically significant relationships are in bold; N/A denotes analyses were not be tested due to insufficient data

	Density (fish/10m²)			**Biomass (g/cm/10m²)**		
	p	**r²**	**Direction**	**p**	**r²**	**Direction**
Blackeye Goby	0.306	0.048	No	0.678	0.008	No
Blue Rockfish	0.215	0.069	No	**0.041**	0.176	**Positive**
Painted Greenling	0.600	0.013	No	0.658	0.009	No
Pygmy Rockfish	0.221	0.067	Positive	0.308	0.047	Positive
Rosy Rockfish	0.299	0.049	No	0.364	0.038	No
Squarespot Rockfish	0.211	0.070	Positive	**0.025**	0.208	**Positive**
Starry Rockfish	0.176	0.082	Positive	**0.005**	0.309	**Positive**
	Mean Length (cm)			**Length Distribution**		
	p	**r²**	**Direction**	**p**	**D**	**Direction**
Blackeye Goby	0.716	0.006	No	0.812	0.073	No
Blue Rockfish	0.212	0.070	No	0.718	0.205	No
Painted Greenling	0.080	0.133	Positive	1.000	0.131	No
Pygmy Rockfish	0.721	0.006	No			
Shallow				N/A	N/A	N/A
Deep				**< 0.001**	0.140	**Positive**
Rosy Rockfish	0.275	0.054	Positive	1.000	0.043	No
Squarespot Rockfish	**0.033**	0.191	**Positive**	**0.033**	0.232	**Positive**
Starry Rockfish	**0.002**	0.358	**Positive**	0.959	0.209	No


a
Blue Rockfish
Biomass (g/cm/10m²)
p = 0.04
r² = 0.18
Area (m²)
Squarespot Rockfish
Residuals of Biomass and Depth
p = 0.02
r² = 0.21
Area (m²)
Starry Rockfish
Residuals of Biomass and Depth
p < 0.01
r² = 0.31
Area (m²)
b
Squarespot Rockfish
Residuals of Mean Length and Depth
p = 0.03
r² = 0.19
Area (m²)
Starry Rockfish
Residuals of Mean Length and Depth
p < 0.01
r² = 0.36
Area (m²)
Pygmy Rockfish (Shallow < 55 m)
Low (n = 0)
High (n = 1136)
p = NA
Relative Frequency
Size Class (cm)
Pygmy Rockfish (Deep > 65 m)
Low (n = 4201)
High (n = 888)
p < 0.01
Relative Frequency
Size Class (cm)

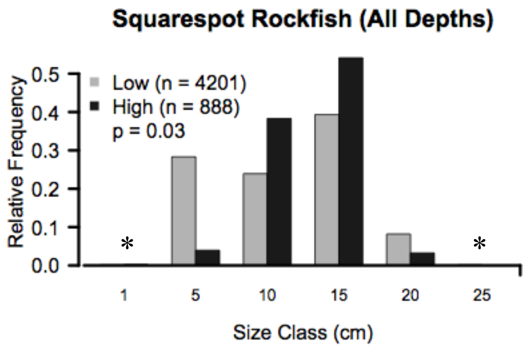


Fig. 13 Comparison of biological response variables (biomass, mean length, and length distributions) of specific species with respect to patch size of rocky bank patches near Point Lobos. Results of biomass analyses are for Blue, Squarespot, and Starry Rockfish (a), the mean length of Squarespot and Starry Rockfish (b), and the length distributions of Pygmy and Squarespot Rockfish (c). If the species index was significantly correlated with depth, the analysis was run with the residuals or the binned data. Gray denotes the low area category and black denotes the high area category. Significant linear relationships are denoted by a dotted regression line. Standard error is plotted as vertical bars. Asterisks indicate size classes in which fish were observed in abundances too small to be observed on the relative frequency histograms. P-values, and where applicable r^2 values, are included in the legends

Regional Comparisons

The similarity of the species composition between Point Lobos and Point Sur was 0.638 (Fig. 14). Although there were regional differences in the specific species present and their proportional abundances, the assemblage composition within central California was similar between these two regions. For most of the assemblage indices, the significance and direction of the relationship between the biological response variables, at the assemblage level, and the independent habitat variables were similar between regions. However, regional differences with respect to edge proximity and patch shape were observed.

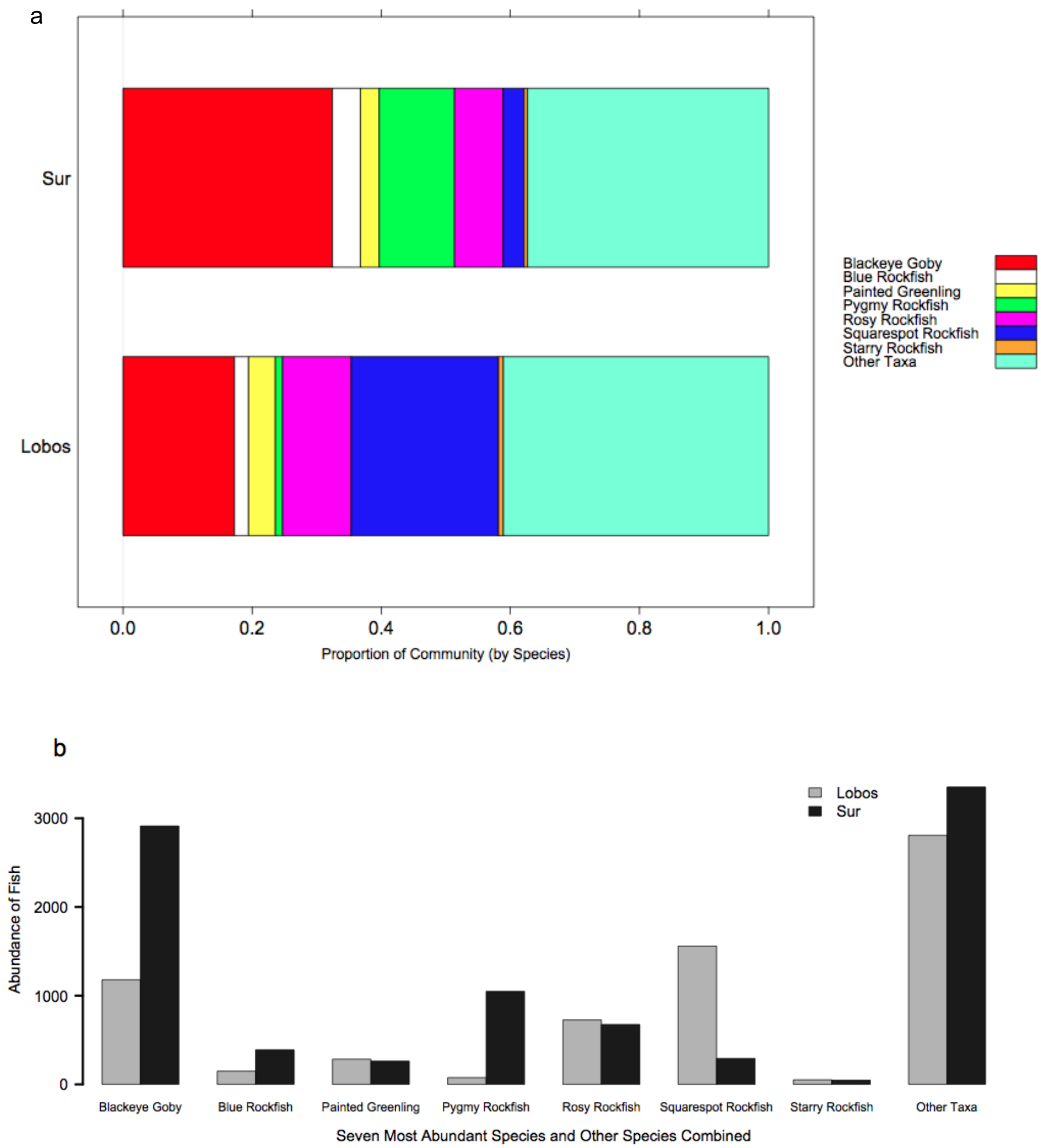


Fig. 14 Species composition of the seven most abundant species for shallow rocky bank patches near Point Lobos and Point Sur. The assemblage composition in proportional abundance (a) and the observed abundance (b) are reported. The unidentified fishes, those not identified to the species level, and the 51 less-abundant species (whose abundance was less than 1% of the total abundance) are pooled into the "other" category

Proximity to Edge. The density of all fishes was not significantly different between the edge and interior zones near Point Lobos (Tables 4 and 13) or near Point Sur ($p = 0.753$; Fig. 15a). Mean biomass was not significantly different between the edge and interior zones near Point Lobos ($p = 0.463$; Fig. 15a) or near Point Sur ($p = 0.958$; Fig. 15b). Similar to the density and biomass results, patterns in the species richness in the nearshore fish assemblage near Point Lobos and Point Sur were not significantly different between the edge and interior zones ($p = 0.061$ and $p = 0.888$; Table 13). However, the observed patterns of the remaining assemblage diversity indices varied between near Point Sur and those observed near Point Lobos. The evenness and heterogeneity near Point Lobos were significantly greater in the edge zone than the interior near Point Lobos (Table 4). Near Point Sur there was no significant difference in evenness ($p = 0.155$) or heterogeneity ($p = 0.465$) between the edge and interior zones of the rocky bank patches.

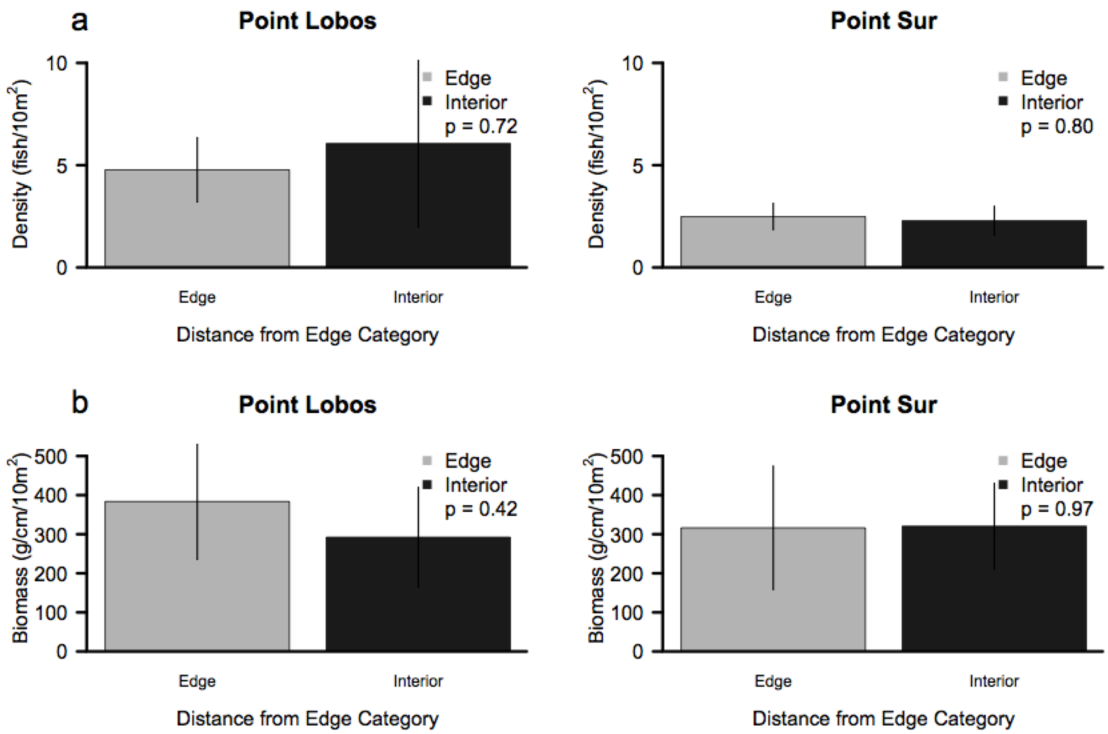


Fig. 15 Comparison of assemblage biological response variables (density and biomass) with respect to distance from rocky bank patch edge near Point Lobos and Point Sur. The results include the assemblage density (a) and biomass (b) between the edge and interior zones of shallow rocky bank patches near Point Lobos and Point Sur. Gray denotes the edge zone and black denotes the interior zone. Standard error is plotted as vertical bars. P-values are included in the legends

Table 13 Assemblage biological response variables (density, biomass, richness, evenness, and heterogeneity) of shallow rocky bank patches near Point Lobos and Point Sur. The results are with respect to proximity to edge (a), patch shape (b), and patch size (c). If the assemblage index was significantly correlated with depth, the analysis was run against the residuals. Statistically significant relationships are in bold

a	**Point Lobos**				**Point Sur**			
	p	**df**	**F-ratio**	**Direction**	**p**	**df**	**F-ratio**	**Direction**
Density (fish/10m2)	0.989	2	0.000	No	0.753	2	0.101	No
Biomass (g/cm/10m2)	0.463	2	0.555	No	0.958	2	0.003	No
Richness	0.061	2	3.865	No	0.888	2	0.020	No
Evenness	**0.008**	2	8.484	**Edge**	0.155	2	2.156	No
Heterogeneity	**0.027**	2	5.584	**Edge**	0.465	2	0.552	No

b	**Point Lobos**			**Point Sur**		
	p	**r^2**	**Direction**	**p**	**r^2**	**Direction**
Density (fish/10m^2)	0.393	0.001	No	0.441	0.055	No
Biomass (g/cm/10m^2)	0.616	0.024	No	0.185	0.154	No
Richness	**0.024**	0.385	**Negative**	0.169	0.165	No
Evenness	0.981	< 0.001	No	0.169	0.165	No
Heterogeneity	0.080	0.252	No	0.848	0.004	No

c	**Point Lobos**			**Point Sur**		
	p	**r^2**	**Direction**	**p**	**r^2**	**Direction**
Density (fish/10m^2)	0.674	0.017	No	0.533	0.036	No
Biomass (g/cm/10m^2)	0.206	0.141	No	0.214	0.137	No
Richness	**0.012**	0.447	**Positive**	0.070	0.268	No
Evenness	0.860	0.003	No	0.554	0.033	No
Heterogeneity	0.088	0.242	No	0.793	0.007	No

Patch Shape (P:A Ratio). The density and biomass of the nearshore fish assemblage did not vary with respect to the P:A ratio near Point Lobos ($p = 0.939$, $p = 0.616$; Table 13) or near Point Sur ($p = 0.441$, $p = 0.185$; Fig. 16a-b). The significant decrease in the number of species observed in rocky bank patches of greater shape complexity near Point Lobos (Table 12) was not observed in the number of species with respect to patch shape near Point Sur ($p = 0.169$; Table 13). The remaining assemblage diversity indices (evenness and heterogeneity) were not statistically related to patch shape either near Point Lobos or Point Sur (Table 13). However, the range of P:A ratios of the rocky bank patches near Point Sur was smaller than near Point Lobos (Appendix D).

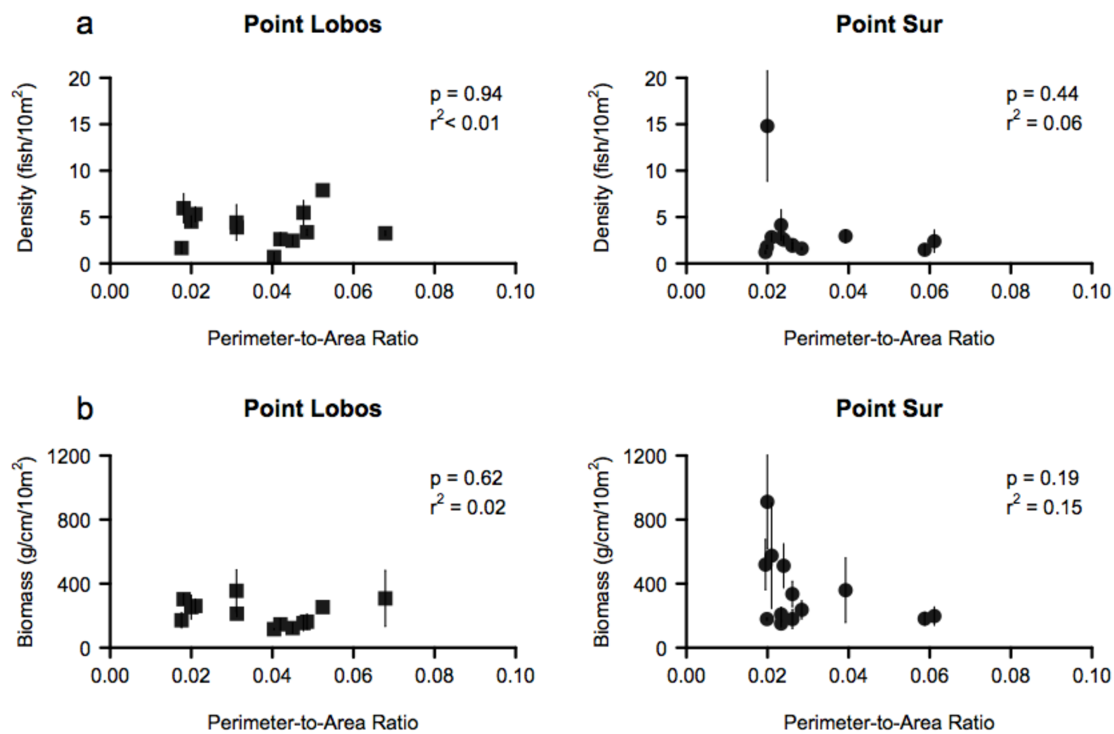


Fig. 16 Comparison of assemblage biological response variables (density and biomass) with respect to patch shape of rocky bank patches near Point Lobos and Point Sur. Results include the assemblage density (a) and biomass (b). Standard error is plotted as vertical bars. P-values and r^2 values are included in the legends

Patch Size (Area). Similar to the relationships among the biological response variables and patch shape, the density and biomass of fishes did not vary significantly with patch area. Similar to the patch shape comparisons, there was no difference in the density or biomass of the assemblage with respect to patch size near Point Lobos ($p = 0.674$, $p = 0.206$) or near Point Sur ($p = 0.533$, $p = 0.214$; Fig. 17a-b, Table 13). Additionally, a significant relationship between species richness and patch size was only observed near Point Lobos (Table 13). Both near Point Lobos and Point Sur there were no significant relationships among evenness or heterogeneity and patch size (Table 13). The range of areas of the rocky bank patches near Point Sur was similar to near Point Lobos (Appendix D).

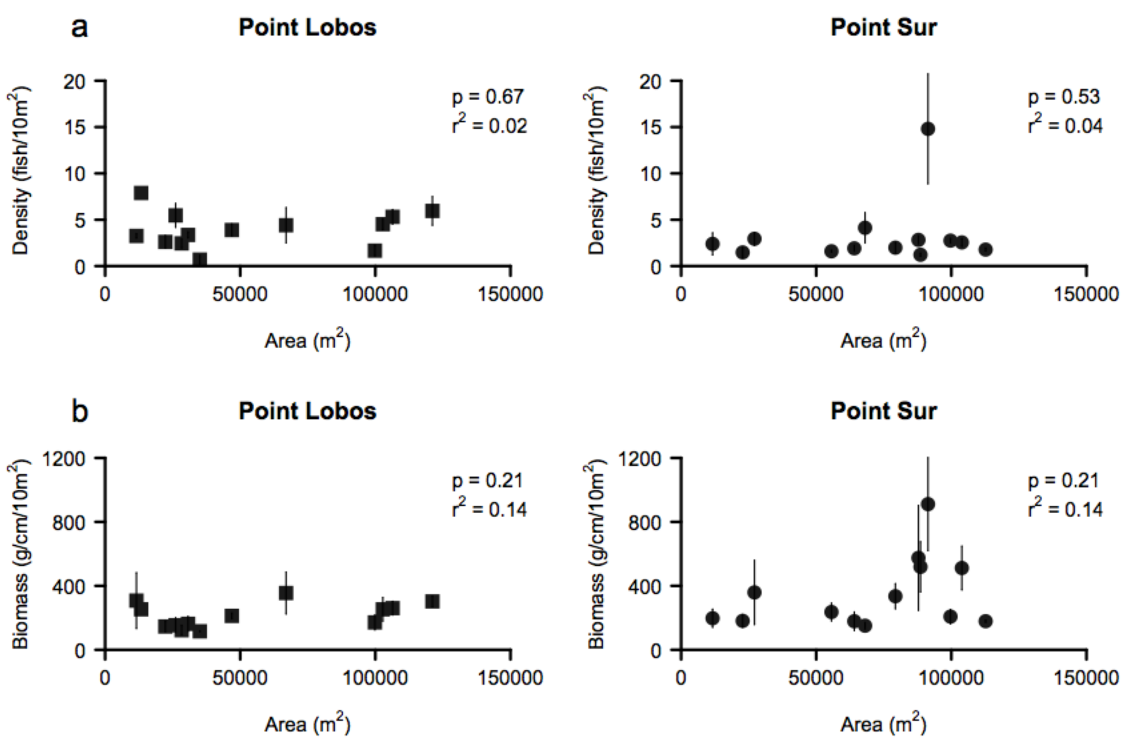


Fig. 17 Comparison of assemblage biological response variables (density and biomass) with respect to patch size of rocky bank patches near Point Lobos and Point Sur. Results include the assemblage density (a) and biomass (b). Standard error is plotted as vertical bars. P-values and r^2 values are included in the legends

Species-Area Relationships

As the rocky bank patch area increased, the number of species increased proportionally. The results of Resampling Statistics indicated that the cumulative number of species observed and the area of fish transects surveyed were similar to that which the species-area relationship equation ($S = c*A^z$) would predict ($c = 159.0$, $z = 0.3$; Fig. 18a). Similarly, results of resampling the cumulative number of species observed and the rocky bank patch area also were similar to those predicted by the species-area relationship equation ($c = 57.87$, $z = 0.25$; Fig. 18b). Additionally the cumulative abundance of the assemblage showed a positive relationship with cumulative area surveyed (Fig. 19a) and rocky bank patch area (Fig. 19b). These results are consistent with the previously mentioned lack of a significant relationship between assemblage density and area, as density is an area-standardized measure of abundance. These results demonstrate that the richness and abundance increases with area within the dataset of this study.

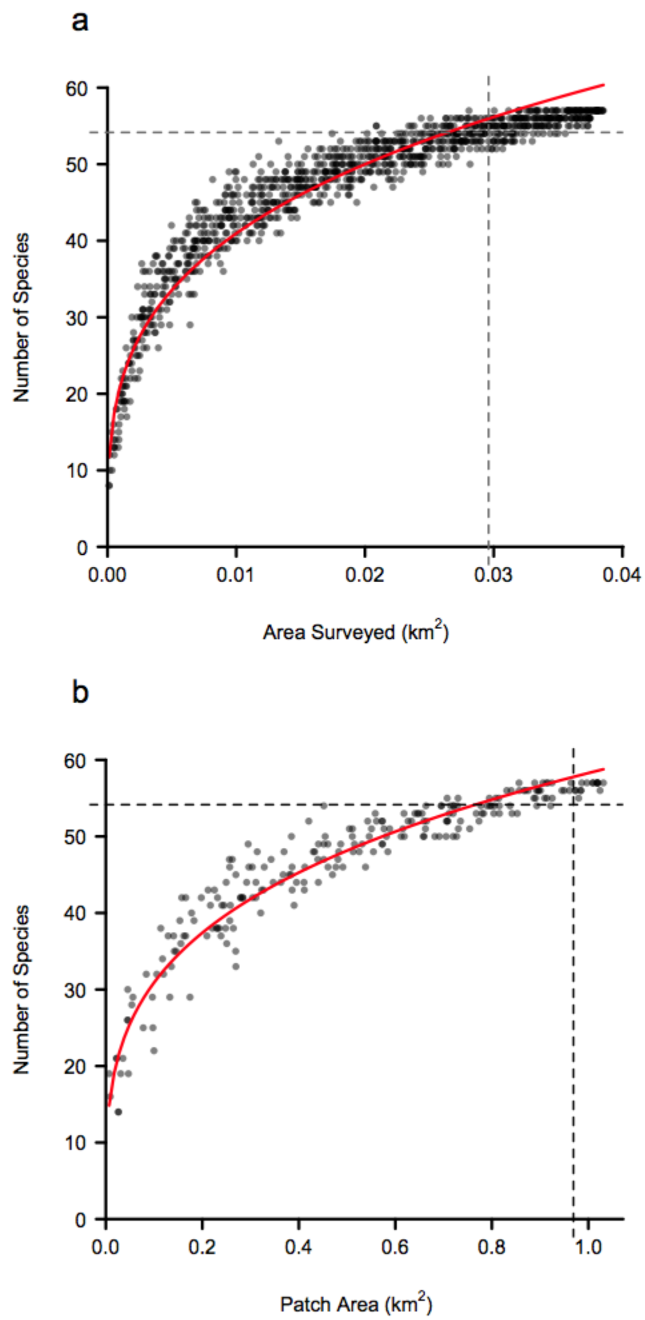


Fig. 18 Cumulative species richness with cumulative area surveyed and patch area near Point Lobos. Results of the resampling analyses of the cumulative species richness with respect to cumulative area surveyed (a) and cumulative patch area (b). The weight of the dot color denotes the frequency of the value in the resampling results. The predicted species-area relationship is superimposed in red. The dotted lines denote 90% of the total number of species and corresponding area surveyed or patch area

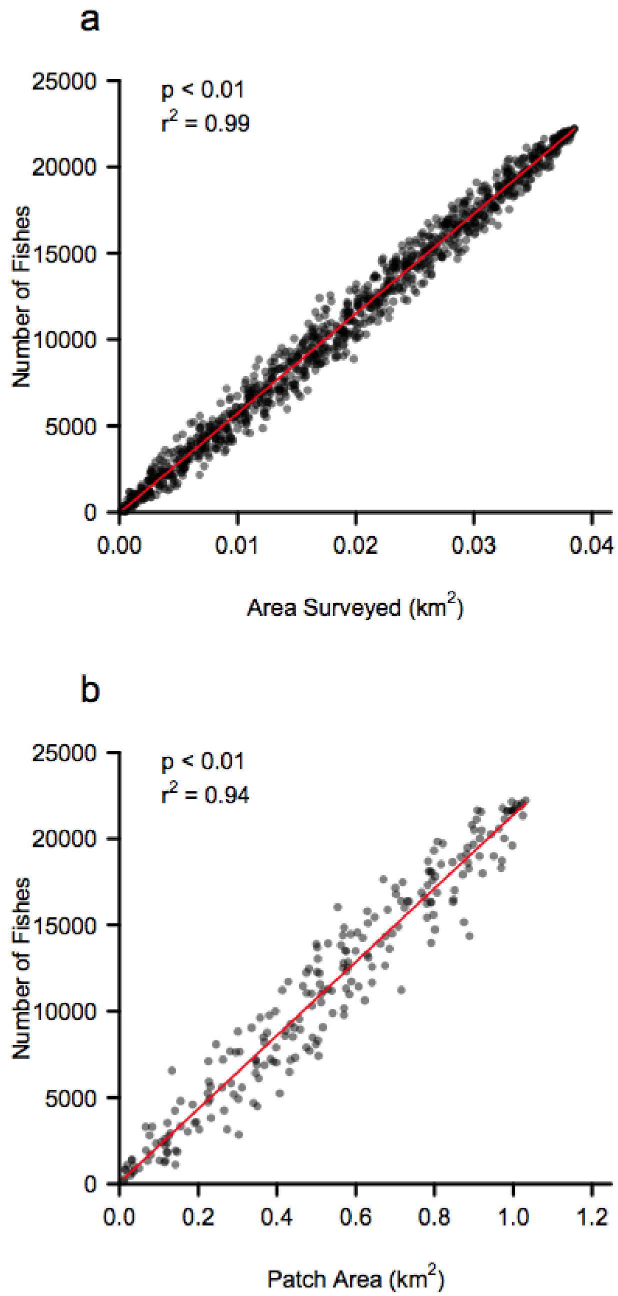


Fig. 19 Cumulative assemblage abundance with cumulative area surveyed and patch area near Point Lobos. Results of the resampling analyses of the cumulative assemblage abundance with respect to cumulative area surveyed (a) and cumulative patch area (b). The weight of the dot color denotes the frequency of the value in the resampling results. The linear relationship of the results is superimposed in red. P-values and r^2 values are included in the legends

Discussion

Does the abundance, diversity, or length frequency of fishes increase with depth?

Previous studies of fish-habitat relationships along the west coast of the United States have highlighted the importance of depth as a factor that explains the presence and abundance of specific species and thus the assemblage composition. My results indicated that there are species-specific differences with respect to depth, yet overall assemblage abundance and diversity increase with increasing depth. This means that more fishes and higher species counts were observed at greater depths. Faunal breaks along the California coast are largely defined by latitude and depth (as reviewed by Allen et al. 2006). This study was limited to the central California coast, and thus there was no effect of latitude on the species assemblage. For central and northern California, the peak fish abundance usually occurs in deep reefs and on the continental slope (Allen et al. 2006), which occur at the deepest limit of the present study region. Therefore, even though this study was constrained to the mid-depth rocky habitat zone (30 – 100 m), significant relationships between assemblage density and biomass with depth were observed. The response of each of the four species groups to depth aligned with previous findings (Miller and Lea 1976, Love et al. 2002, Allen et al. 2006).

Patterns in the species-specific density with respect to depth also aligned with previous research. For example, Blue Rockfish often are found in sub-tidal reefs and rocky habitats in less than 90 m depth (Love et al. 2002). In this study, Blue Rockfish were more abundant in shallow rocky bank patches, and density decreased with depth towards 100 m, which is outside of the habitable depth of the species. In contrast, Starry Rockfish are typically found between 60 and 150 m of water (Love et al. 2002) and thus would, on average, peak in abundance around 100 m of depth. In this study, the density of Starry Rockfish significantly increased with depth toward the 100 m depth range of the study.

Assemblage composition naturally varies with depth due to individual species-specific depth ranges. As with fish abundance, there is a positive relationship between richness and depth across the continental slope (Allen et al. 2006). Therefore, it was expected to observe a positive relationship between the number of species and depth near Point Lobos. However, this kind of relationship was not observed. Perhaps the depth range of this study was not wide enough to observe the depth ranges of highest species richness, or the topography of Point Lobos may limit the overlap of species depth ranges. Most of the deep rocky bank patches within this study were located at the top of canyon walls. Rather than a gradual decrease in depth that fosters species overlap, the canyon walls might act as a barrier to the overlap of species or our ability to observe the overlap from the submersible.

Fish assemblage diversity often increases with increasing depth (Chittaro et al. 2010). However, this pattern was not observed within the mid-depth rocky habitat zone, which again could be due to the narrow depth range of this study. Evenness decreased with depth, meaning that a few species were more dominant in the deeper rocky bank patches. For a similar reason, the overall diversity of the assemblage decreased with depth. The difference in these results versus previous studies investigating the assemblage structure across the continental shelf could be because the depth range in this study was shallower than in previous studies of the nearshore fish assemblage.

The relationships among mean length and depth observed for the specific species supported previous findings. The increase in mean lengths of the dwarf rockfishes (Pygmy, Rosy, and Squarespot Rockfish) with depth is consistent with observations of younger rockfishes inhabiting shallow waters and moving to deeper habitats with age (Love et al. 2002). These ontogenetic shifts with depth are well documented for species within the large rockfish and non-rockfish species group: Yelloweye Rockfish (*S. ruberrimus*, Cramer 1895; Richards 1986, O'Connell and Carlile 1993), Bocaccio (*S. paucispinus*, Ayres 1854; Allen et al. 2006), and Lingcod (*Ophiodon elongatus*, Girard 1854; Fields 2005). However, the length distributions of these species groups in this study did not vary with respect to depth. This may be due to the 100 m depth restriction. The submersible transects analyzed covered the shallower portions of the depth range of these species and most likely the smaller lengths of the individuals for many of these species. For example, Love et al. (2002) reported that Yelloweye Rockfish were most abundant between 90 and 180 m and Bocaccio between 50 and 250 m; thus, it was expected to see individuals of shorter lengths at the shallow end of their range, which was the deeper portion of the depth range in the present study.

The increase in the density of the assemblage and the decrease in the diversity with respect to depth support the previous conclusions that habitat depth strongly influences assemblage composition in California (Allen et al. 2006). Although a large portion of the variability (22 to 42%) is explained by depth, this study was interested in what other variables could be influencing the variation in the nearshore fish assemblage. An additional factor that previous researchers have correlated with species composition of the fish assemblage is the complexity of the fine-scale habitat.

Does the abundance, diversity, or length frequency of fishes increase with rugosity?

Previous investigations of the nearshore fish assemblage have illustrated a relationship between fine-scale habitat types and the abundance and presence of specific species within the mid-depth rocky habitat zone (Ralston et al. 1986, Pearcy et al. 1989, Stein et al. 1992, Yoklavich et al. 2000, Anderson and Yoklavich 2007). Gratwicke and Speight (2005) used rugosity as a quantifiable metric to investigate the relationship between fine-scale habitat types and the fish assemblage. As a habitat type becomes more complex, the surface area of the seafloor increases and provides increased refuge from predators (Hixon and Beets 1989, Irlandi et al. 1995, Wilson et al. 2008), increased foraging opportunities (García-Charton et al. 2004), and increased niche partitioning (MacArthur and Levins 1964). Therefore, this study expected to observe a positive relationship among all of the biological response variables and rugosity.

The importance of fine-scale habitat type complexity is evident in the relationships this study observed among length frequency distributions of the species groups and specific species and rugosity. These results indicated that the length distribution of fishes was skewed towards shorter individuals in less complex habitat and longer individuals in more complex habitat. Previous studies have shown that Atlantic Cod (*Gadus marhua*, Linnaeus 1758) and Nassau Grouper (*Epinephelus striatus*, Bloch 1792) demonstrate ontogenetic shifts in the complexity of habitats they use (Gotceitas and Brown 1993, Gotceitas et al. 1995, Dahlgren and Eggleston 2000). Additionally, work with Atlantic Cod demonstrated that juveniles and adults rely on different defense mechanisms within soft sediment and complex rocky habitats, which could explain the pattern of longer individuals using more complex habitat (Gregory and Anderson 1997). However, there was no relationship among the other assemblage indices (density, biomass, or species composition) and rugosity. Therefore, fine-scale variation of the habitat does not appear to be a major factor affecting assemblage structure across the landscape of this study area.

Although rugosity was not correlated with many of the assemblage indices, significant relationships among density and length distributions of fishes were observed in the four species groups and species-specific analyses. In other studies, species within the other benthic species group have shown a positive correlation with rugosity (Yoklavich et al. 2002). Whereas the density dwarf rockfishes did not correlate with rugosity in this study, a previous study reported a positive association of abundance with rock, boulder, and cobble substrata (O'Farrell et al. 2009). Additionally the abundance of Blue Rockfish, which are semi-pelagic but have been previously reported to associate with rock pinnacles (Jorgensen et al. 2006), negatively correlated with rugosity. Although these results seem to counter those of Jorgensen et al. (2006), no pinnacles were included in this study.

The significant relationships among the species groups and specific species with respect to rugosity support previous findings that rugosity is an important factor in species-specific responses to habitats. When there was a significant relationship, rugosity only explained 19% to 24% of the variability. However, these results also suggest that the assemblage as a whole is not strongly affected by rugosity across a landscape scale. Therefore, less than 50% of the variability in assemblage structure was explained by depth and rugosity in this study. Other observable factors, such as the independent habitat variables of the rocky bank patches, may account for the remaining variation in the nearshore fish assemblage.

Does the abundance, diversity, or length frequency of fishes increase with respect to the proximity of the edge of a rocky bank patch as would be predicted by the terrestrial landscape paradigm?

There is no standard ecological method for choosing the width of an edge zone. Previous landscape-scale investigations have defined the edge zone based upon the highest observed density (Peterson and Turner 1994), by using what other studies have used (Bologna and Heck 1999, Tanner 2003), or by slightly increasing the distance used by other studies (Jelbart et al. 2006). Therefore, designing an objective method for defining the edge zone for the rocky bank patches was a priority of this study. This study investigated both species-specific and assemblage responses to the edge, and thus the movement patterns of individual species could not be used to define the edge zone, as home range varies with body size (Kramer and Chapman 1999) and across species (NOAA 2004). Using the edge-width distance from previous studies would have enabled comparisons of the results from this study with those studies. However, most marine studies have used a distance that was defined by the distribution of epifaunal invertebrates in seagrass meadows (Peterson and Turner 1994, Bell et al. 1995). Therefore, assemblage density and the richness per unit area surveyed was used, two metrics that had been used previously to define the edge zone width, to look objectively for break points in the data. Both of these variables suggested a similar edge width zone. This width resulted in a similar percentage of the patch area being defined as the edge as compared to a previous seagrass study of fishes (Jelbart et al. 2006). In addition, the edge width used was at a similar scale to the estimated horizontal foraging range of Señorita (*Oxyjulis californica*, Günther 1861), another temperate fish (Bernstein and Jung 1979).

Terrestrial studies have reported increases in density and biomass of individuals along the edges of habitat patches within a landscape (Lidicker 1999, Bolger et al. 2000, Golden and Crist 2000). However, to date, marine studies have shown conflicting results with respect to the density of organisms at a patch edge. Changes in density at the edge of a habitat patch could be due to niche overlap of species at the edge or predator distribution and movements. For example, some researchers have observed an increase in total density of species due to a decrease in susceptibility to predators along edges (Gotceitas and Brown 1993, Fraser et al. 1995, Gotceitas et al. 1995, Gregory and Anderson 1997) and attributed this to decreased foraging efficiency of predators along edges (Hovel and Lipcius 2001). Other studies reported an increase in access to prey by predators along edge boundaries (Irlandi 1994), and a subsequent increase in predator density (Holmes and Laundré 2006) or preferential use of the edge area by predators (Carfagno et al. 2006, Heithaus et al. 2006, Papastamatiou et al. 2009).

In the rocky bank patches of this study, there was no difference in the density or biomass of the assemblage between the edge and interior zones of shallow rocky bank patches. However, there was an increase in both density and biomass at the edge in deep rocky bank patches. The increase in density and biomass of fishes at the edge could be due to direct selection of the edge zones by fishes or an indirect correlation of density with the edge zone, as explained by Wiens (1976). Regardless of whether the presence of fishes of the nearshore fish assemblage in close proximity to the rocky bank patch boundary is due to direct or indirect factors, these results indicate that edge effects do occur in deeper waters of the ocean than had previously been studied. Additionally, these results further document edge effects related to fish assemblage structure in temperate non-vegetative habitats.

Patterns with respect to the distance from a rocky patch boundary are not static, but rather may be influenced or driven by fine-scale movement patterns of individual fish. Lowe and Bray (2006) and Freiwald (2010) both synthesized current literature on movement patterns of fishes, concluding that the timing of movements and activity patterns vary among fish species and individuals within a species. Multiple biological (e.g., competition, prey or predator presence) and environmental (e.g., habitat quality, lunar phase, water temperature) variables have been correlated with movement patterns of fish. Whereas we are gaining an increased understanding of the size of home ranges, the total area used over time; unfortunately, little work to date has focused on the fine-scale daily movement patterns of fish. It is at this scale, of hourly or daily movements, in which the patterns with respect to the distance to rocky bank patch boundaries would be observed. Therefore, future work should focus on investigating fine-scale movement patterns with respect to landscape-scale habitat characteristics.

The lack of edge effects related to density or biomass in shallow patches suggests that different processes may affect the assemblage structure in shallow rocky bank patches as compared to seagrass meadows or terrestrial habitats. Positive edge effects related to eelgrass assemblage density have been attributed to increases in foraging opportunities (Irlandi et al. 1999, Hovel and Lipcius 2001). Patterns of increased density at the edge also have been linked with the increase in food availability at the seagrass edge as the blades dampen the currents (Bologna and Heck 2002). In this study of shallow rocky bank patches, the distribution of dwarf rockfishes, the prey species for larger fishes in the nearshore assemblage, was higher in the interior. Several reasons could explain the increase in prey items in the interior of rocky bank patches. First, prey species may seek refuge from predators in the interior of patches. Irlandi et al. (1999) reported that predation rates decreased with increasing distance from the edge zone. Second, if food is not a limiting resource for prey species because it is advected across all portions of the rocky bank patch, rather than only available at the edge zone, then there may be more food items for the prey species within the interior of the patch. Third, further research is needed to determine if predatory species have greater foraging success at the edges and thus the density of prey species is reduced at the edges of rocky bank patches.

The increase in the density of predatory species, such as large rockfishes, at the edge may be due to the presence of prey species in the adjacent habitats. For other species there was no difference in the density of individuals between the edge and interior as would be expected from previous research. For example, Jorgensen et al. (2006) observed Blue Rockfish most often 10 – 20 m from the kelp forest edge. In this study there was no edge effect related to Blue Rockfish, possibly because they occurred more often in the buffer (12 – 36 m from the rocky bank patch boundary).

Similar to terrestrial studies (Yahner 1988), there was a positive edge effect related to diversity of the nearshore fish assemblage throughout the depth range. The increase in diversity could be indicative of species overlap between rocky habitat fishes and soft bottom fishes occurring at the edge of rocky bank patches in the mid-depth rocky habitat, as seen in other systems (Ward et al. 1999, Baker et al. 2002). Indeed, species that associate with soft sediment, e.g., flat fishes, only were observed in the edge zones of rocky bank patches. In addition to these overlapping species, there also were species that occurred only in the edge or interior zones of the rocky bank patch (Appendix H). For instance, Big Skate (*Raja binoculata*, Girard 1855), Spotted Scorpionfish (*Scorpaena guttata*, Bloch 1789), and Yelloweye Rockfish[4] were present only in the edge zones near Point Lobos. Whereas, Bank (*S. rufus*, Eigenmann and Eigenmann 1890), Rosethorn (*S.*

[4] It is important to note that the sample size for Yelloweye Rockfish in the edge zone was very small. Many of the Yelloweye Rockfish were observed in the buffer (12 – 36 m from the rocky bank patch boundary).

helvomaculatus, Ayres 1859), and Shortbelly (*S. jordani*, Gilbert 1896) Rockfish were observed only in the interior zones. Furthermore, there were fewer dominant species in the edge zone in both shallow and deep rocky bank patches than in the interior zone. The increase in species evenness further suggests that there is an overlap of species from both rocky and soft bottom habitats. An increase in the diversity of the assemblage at the edge of a rocky bank patch results from both an increase in the number of species and a decrease in the dominance by individual species within the assemblage.

In terrestrial studies, researchers have observed an increase in the size of individuals along the edges due to a higher proportion of large predators (Woodroffe and Ginsberg 1998) or avoidance by smaller organisms of the edge zones (Foster and Gaines 1991). The higher density of a large predatory species group (large rockfishes) suggests that there are a higher proportion of large predators in the assemblage at the edge.

The similarity in density between edge and interior zones in shallow rocky bank patches indicates that different processes could be driving the increase in large fishes at the edge in different depths of rocky bank patches than those observed in shallow seagrass meadows. There could be increased competition from other large fishes along the edges, which potentially explains the lack of a pattern observed in shallow patches. The positive edge effect in deep patches could indicate that large predatory fish may travel farther to forage off of the rocky bank patch. For example, studies of tropical predatory fishes have observed off-reef foraging patterns of fishes that seek refuge in the reef (Frazer and Lindberg 1994, Posey and Ambrose 1994). Therefore, the observed positive edge effect could be due to their feeding habits off of the rocky habitat, not due to the food availablity at the edge of the rocky bank patch. Conversely, the increase in large predatory species at the edge could be because aggregations of prey items, such as zooplankton, micronekton, and small fish, often occur near abrupt topographic changes, like a rocky bank patch edge (see review by Genin 2004). Additionally, many rocky habitats in the central California coast have ledges around the edges of the habitat. These features could indicate more efficient shelter opportunities at the edges of rocky bank patches for larger fishes.

The density, diversity, and length results this study observed generally support previous landscape-scale studies in both terrestrial and marine systems. However, it seems that the ecological processes that are driving the edge effects differ across ecosystems. Similar to what Fagan et al. (1999) suggested, this study demonstrates a need for further work to focus on quantifying the key processes, e.g., food availability or refuge, which shape the nearshore fish assemblage across a landscape.

These results also have important implications for how scientists survey the nearshore fish assemblage. To increase the accuracy of our assemblage characterization it is important to conduct surveys of the fish assemblage throughout both the edge and interior zones of the rocky bank patches. If surveys only occur in the interior or at the edge of the rocky bank patch then those surveys would produce biased estimates of the fish assemblage. Starr et al. (1996) highlighted a potential bias of using a submersible when quantifying the nearshore fish assemblage. They reported greater abundances of fishes, especially semi-pelagic and pelagic fishes, more than 2 m off seafloor, outside the scope of the submersible surveys. These results indicate that the observed differences between the edge and interior zones of rocky bank patches within this study may be stronger for other portions of the nearshore fish assemblage than we are able to survey using a submersible.

Does the abundance, diversity, or length frequency of fishes increase with respect to the shape of a rocky bank patch?

The presence of edge effects related to the fish assemblage structure in sub-tidal rocky habitats indicates that the shape of the rocky bank patch should also affect the distribution and abundance of fishes. As the rocky bank patch boundary gets more complex, the proportion of the rocky bank patch that is within the edge zone increases. Due to the difficulty in and subjectivity of defining the edge width for a habitat patch and because it is easier to assess the shape of a rocky bank patch when developing a sampling design, it would be advantageous to use the shape of a rocky bank patch to account for the observed edge effects in future studies to assess the nearshore fish assemblage. Unfortunately, the shape of rocky bank patches did not significantly correlate with the density, diversity, or lengths of species within the fish assemblage in the rocky bank patches in this study. Therefore, patch shape is not a predictive indicator for most biological response variables.

Although the patch shape of rocky banks did explain roughly one quarter of the variability in species richness, it was not in the direction that was expected. The edge analyses revealed an increase in richness at the edge zones. Therefore, it was anticipated that as the shape of the rocky bank patch got more complex there also would be an increase in the number of species because there would be an increase in the amount of patch that occurred in the edge zone. However, fewer species were observed as the rocky bank patch shape increased in complexity.

The seemingly contradictory results of the rocky bank patch shape analyses may indicate that the patterns of foraging or dispersal are different on rocky banks than in terrestrial habitats. In terrestrial studies, researchers have correlated the shape of habitat patches with increased dispersal and foraging of organisms (as summarized by Forman and Godron 1986, Gutzwiller and Anderson 1992). In the ocean, currents advect food particles through the water column and thus organisms forage differently in the oceans (Cowen and Sponaugle 2009). Whereas habitat patch shape can be a predictor of the distribution of species on land, it may not be relevant in the marine environment because underlying food dispersal processes are different.

Alternatively, the range of P:A ratios within this study may not be wide enough to detect the influence of rocky bank patch shape on the biological response variables. Although the P:A ratio values of the rocky bank patches were 1.4 to 2.5 times more complex than a perfect circle of similar area, perhaps the effect of boundary complexity does not influence species distribution until it is of greater complexity. In addition, P:A ratio and area were highly correlated, and therefore rocky bank patch size might be more of a factor driving assemblage structure. Previous marine studies also did not observe significant relationships among the biological response variables and the shape of seagrass patches, but reported that biological response variables were correlated with seagrass patch size (Jelbart et al. 2006). This could also explain why the signal of edge effects was not observed in all biological response variables of the assemblage for the rocky bank patch shape analyses.

Rocky bank patch shape did correlate with the number of species and the proportion of large individuals observed throughout rocky bank patches. In addition, the species-specific analyses illustrated that the complexity of the rocky bank patch boundary can be a predictor of the size composition, but not other biological response variables at the species group or species level. The species-specific relationships with rocky bank patch shape did not match results from the edge analyses either. For example, even though there were higher densities of Blackeye Goby observed at the edge of rocky bank patches, there was no relationship between this species and rocky bank patch shape. This could be because the home range of Blackeye Goby is small in comparison to other species and thus it is almost always at the edge of the microhabitat it associates with.

These results have important implications for the design of surveys to assess the diversity of the nearshore fish assemblage. Because the length frequencies of fishes and the number of species change in response to the complexity of the boundary of rocky bank patches, it is necessary to stratify a sampling scheme throughout a range of rocky bank patch shapes. Surveying within multiple rocky bank patch shapes would increase the accuracy of the assemblage structure estimates for the region, thus the shape of rocky bank patches should be considered when developing the sampling design for a survey.

Does the abundance, diversity, or length frequency of fishes increase with respect to the size a rocky bank patch?

Previous marine landscape studies determined that the size of habitat patches was a greater factor in explaining assemblage structure than the shape of the habitat patch (Eggleston et al. 1998, Bolger et al. 2000, Jelbart et al. 2006). The results from this study support these conclusions. Whereas rocky bank patch shape explained roughly a quarter of the variability in the number of species observed, the size of the rocky bank patch explained 48%. Therefore, the size of a rocky bank patch was a more robust predictor of species richness in the nearshore fish assemblage than rocky bank patch shape. The number of species within the assemblage strongly correlated with area, as would be expected from species-area relationship curves. Additionally, the observed positive relationship between species richness and rocky bank patch size aligns with previous marine and terrestrial studies (Winemiller and Leslie 1992, Elliot et al. 1998, Heegaard et al. 2007).

Rocky bank patch size did not correlate with species density within the assemblage. Although there was a positive relationship between fish abundance and rocky bank patch size, there was no significant relationship between density and rocky bank patch size. These results support the relationship between abundance, density, and area as summarized by Risser (1995). If abundance increases proportionally to the increase in area of patches, there should be no change in density with increasing area, as density is standardized to area (Risser 1995). Additionally, Bender et al. (1998)

suggested that using the total patch size rather than the area that species inhabit within the patch could result in underestimates of density. Future studies should investigate if similar underestimates of the nearshore fish assemblage occur by conducting tracking studies to quantify the proportion of the habitat used.

However, there were differences in the biomass and lengths of four of the species investigated with respect to rocky bank patch size. In fact, three rockfish species demonstrated an increase in biomass with increasing area. Therefore, individual species responded uniquely to the area of rocky bank patches. Sampling measures of the assemblage need to account for such species-specific differences when generalizing about patterns with respect to patch size across a landscape.

Similar to rocky bank patch shape, the size composition of the nearshore fish assemblage varied with area at the species group and species-specific level. Interestingly, there was a significant increase in the proportion of individuals of longer lengths with increasing rocky bank patch size, both for a species group and for individual species. The increase in lengths of fishes could be due to ontogenetic shifts to larger rocky bank patches with greater size due to an increase in home range requirements. Larger fishes often need a greater area to encounter enough prey to survive. Larger individuals of rocky habitat-specific species, such as Squarespot Rockfish, were observed in higher proportions in rocky bank patches of greater area. In addition, rocky bank patch size also varied with other biological response variables for some but not all species.

The relationship between the size of patches and the number of species has important sampling design implications. To survey accurately the nearshore fish assemblage across a landscape, it is necessary to include a range of rocky bank patch sizes, as the number of species does not increase linearly with an increase in area. Additionally, to quantify the biomass of the assemblage or the range of sizes of fishes throughout a landscape one would need to stratify the sampling design across rocky bank patches of various areas.

Are patterns in the nearshore fish assemblage with respect to independent habitat variables similar between regions of the central California coast?

The results from Point Lobos suggest that researchers need to account for independent habitat variables when investigating the nearshore fish assemblage. It is also important to understand if these relationships between assemblage structure and the landscape are specific to the Point Lobos area or if they can be generalized throughout central California. This study expected that the magnitude of the patterns would differ among regions due to differences in region-specific characteristics, but that the direction of the patterns would be similar. If the observed patterns occur in multiple regions, these results can be applied widely to current research projects collecting information for fisheries management.

Results for the biological response variables at the assemblage level of nearshore fishes were relatively similar between the two regions. There was no difference in the response of density between the two regions. However, the increase in the biomass of fishes in the edge zone was only observed near Point Lobos. This difference between the two regions could be due to differences in their topography. The topography of Point Lobos is interspersed with canyon heads, whereas Point Sur is a large shelf (Fig. 1). These differences could affect the advection and distribution of food items. For example, if stronger currents near Point Sur advect more food towards fishes, there could be less of a need for larger individuals to stay at the edge of rocky bank patches.

The assemblage responses to the shape and size of the rocky bank patch were similar between the two locations. For example, the shape of the rocky bank patch did not correlate with the density or biomass in either Point Lobos or Point Sur. The relationships between assemblage variables and rocky bank patch size were consistent between the two regions. This further suggests that the area of the rocky bank patches drives much of the variability in the nearshore fish assemblage.

These results demonstrate the importance of investigating patterns in assemblage structure in multiple places throughout the region, as well as against multiple independent habitat variables. The pattern of the relationships among the biological response variables and the independent habitat variables were in a similar direction near Point Lobos and Point Sur. This indicates that the patterns in the nearshore fish assemblage with respect to landscape-scale habitat variables are most likely similar throughout central California.

What are the management implications of the observed patterns in nearshore fish assemblages with respect to landscape-scale habitat characteristics?

The spatial scales at which researchers collect fishery data, at which fish interact, and at which we manage our fisheries are substantially different. Most researchers investigate assemblages of nearshore fishes at a scale smaller than the functional subpopulations of species. However, we manage fisheries at scales larger than the spatial area of subpopulations. By determining how assemblages and individual species respond to independent habitat variables across a landscape, we are able to gain a better understanding of how assemblages of fishes are distributed and how species interact within the assemblage at spatial scales more similar to those of subpopulations. Results from this study therefore have important ecosystem-level implications for fisheries management.

Currently, the data collection technique used in this study is utilized in surveys that inform stock assessments of commercially harvested species (e.g., Yoklavich et al. 2007). This study demonstrated that species are contagiously distributed; higher densities of large rockfishes are disproportionately observed at the edge of rocky bank patches. To accurately estimate the current standing biomass of such species for stock assessments, it is imperative to design sampling schemes that survey the rocky bank patch edges where these species are present. Abundance estimates will be more accurate if sampling is stratified across the landscape based upon knowledge of the non-random patterns of species distribution.

Some fisheries scientists have estimated regional population abundance for stock assessments by multiplying fish density estimates by the amount of available rocky habitat (O'Connell and Carlile 1993). This method holds promise for estimating population sizes and species composition when limited resources are available. However, results from this study demonstrate that species are not uniformly distributed throughout rocky bank patches within the rocky habitat. Depending on the initial sampling location, such techniques could result in biased estimates. For instance, if surveys of commercially important large rockfishes, e.g., Vermilion (*S. miniatus*, Jordan and Gilbert 1880) and Canary Rockfish (*S. pinnger*, Gill 1864) or Bocaccio, were only conducted within the interior of rocky bank patches, the estimates of density would be artificially low because these species are positively correlated with proximity to rocky bank patch edges. Further work investigating species-specific responses to the edge and interior portions of rocky bank patches is necessary prior to fully utilizing the above-mentioned technique of extrapolating population size from habitat availability.

Additionally, these results illustrate that edge portions of rocky bank patches serve an important function in shaping the nearshore fish assemblage. Therefore, area-based management decisions that are intended to protect the community (e.g., MPAs) or the habitat necessary to support these communities (e.g., Essential Fish Habitat) should ensure that these edge zones of rocky bank patches are sufficiently protected. Further studies should attempt to quantify which ecological processes that occur along the edge of rocky bank habitats result in increased density, diversity, and size of individuals.

Other results from these analyses have important implications for area-based management. Two dominant questions in designing effective area-based management approaches are the scale at which management decisions should be made and how to effectively monitor the effects of these management decisions. Results from this study provided information for both of these questions. The significant relationship between species richness and rocky bank patch size demonstrated that as the area of a rocky bank patch increases linearly, the number of species increases non-linearly. If the goal of area-based management is to protect the diversity of the fish assemblage, as estimated by the species richness, this indicates that protecting larger rocky bank patches may be more effective.

Knowing the species-area relationship for central Californian rocky banks leads to the question of what size of rocky bank patches should be protected. Results from this study demonstrated that rocky bank patches that are roughly 0.97 km^2 would protect 90% of the total number of species within the region. Additionally, the relationship between cumulative abundance of fishes and rocky bank patch size provides information about the area necessary to protect a viable portion of the population, once minimum viable population size is known (Gaines et al. 1992). The species-area relationships could be determined for individual species, or for the assemblage, to include in viability analyses. Information from these two data sources would enable managers to define more robust criteria for the amount of area required to protect the nearshore fish assemblage or individual stocks.

The relationship between species richness and area surveyed also provides important information for monitoring area-based management or for assessing the health of the nearshore fish assemblage. The species-accumulation relationships for area surveyed illustrate that at least 0.03 km^2 of a rocky bank patch should be surveyed to observe 90% of the species within the rocky bank patch. Knowing how much of a rocky bank patch to survey would enable researchers to more efficiently allocate their sampling efforts and to increase the accuracy of their estimates of the biological response variables.

These results demonstrate that the size of rocky bank patches is a driving factor in the composition of the nearshore fish assemblage and in our understanding of it. Area-based management is grounded in the importance of the spatial configuration of habitats and species distributions. Research on fish-habitat relationships at the fine scale has, to date, been the primary consideration when protecting the nearshore fish assemblage. However, the results of this study demonstrate that it is imperative to consider landscape-scale habitat characteristics across a landscape, especially habitat patch size. This information will improve our ability to manage fisheries in smaller areas of the coastline.

Conclusions

Landscape-scale research in the marine environment is an emerging field, and additional studies enhance our ability to determine if it is possible to transfer terrestrial models of management to the oceans. The results of this study highlight the similarities and differences among sub-tidal rocky habitat, other marine ecosystems, and terrestrial environments. It is important to consider these differences when attempting to apply ecological patterns across ecosystems. Additionally, having an increased understanding of the response of nearshore fish assemblages to landscape-scale habitat characteristics will enable managers to design more effective area-based management approaches (e.g., MPAs) in terms of their size, shape, and location. Therefore, understanding patterns in fish assemblages across a landscape will improve fisheries management locally as well as regionally.

This study documented that predictable landscape-scale patterns do exist in the distribution of nearshore fish assemblages. For example, there was an increase in the assemblage biomass, richness, and mean length of fishes in the edge zones of sub-tidal rocky bank habitat patches at the landscape scale. Results also indicate that there was a significant increase in the density of large rockfishes at the edge of rocky bank patches. Additionally, there was a significant increase in the species richness of fishes with increasing rocky bank patch size. In fact, rocky bank patch size explained more of the variability in the fish assemblage structure than the shape of the rocky bank patch. These results show that there are patterns in the distributions of nearshore fishes across a landscape. To appropriately survey fishes across a landscape it is imperative to design sampling protocol with an understanding of these patterns.

However, this study also demonstrated that terrestrial paradigms are not directly applicable to the nearshore fish assemblage in temperate sub-tidal marine habitats. The complexity of the rocky bank patch shape was not a good predictive indicator for the nearshore fish assemblage. There were no significant relationships among patch shape and the density or diversity of the nearshore fish assemblage, however the range of patch shapes used in this study may have been too restrictive to observe significant relationships. Although there was a significant relationship between patch shape and species richness, it was a negative relationship rather than the positive relationship repeatedly observed in terrestrial systems. In addition, there was no significant relationship between species density and the proximity to the patch edge for the nearshore fish assemblage. These results highlight that terrestrial paradigms should not be directly applied to the marine environment. Instead, further research should quantify the patterns of nearshore fish assemblage with respect to landscape-scale habitat characteristics.

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Appendices

Appendix A Species observed near Point Lobos and Point Sur, by abundance and percentage abundance. Species in bold, individually make up more than 1% of the total abundance

		Lobos		Sur	
Scientific Name	**Common Name**	**Abundance**	**Percentage**	**Abundance**	**Percentage**
Agonidae	Poacher	1	0.00%	1	0.01%
Anarrhichthys ocellatus	Wolf Eel	0	0.00%	1	0.01%
Bathymasteridae	Ronquil	17	0.08%	15	0.22%
Citharichthys sordidus	Sanddab	5	0.02%	1	0.01%
Cottidae	Sculpin	12	0.05%	1	0.01%
Damalichthys vacca	Pile Surfperch	25	0.11%	12	0.18%
Embiotoca jacksoni	Black Surfperch	9	0.04%	2	0.03%
Embiotoca lateralis	Striped Surfperch	11	0.05%	1	0.01%
Hexagrammos decagrammus	Kelp Greenling	34	0.15%	15	0.22%
Hydrolagus colliei	Ratfish	7	0.03%	1	0.01%
Pleuronectiformes	Flatfishes	4	0.02%	1	0.01%
NA	Unidentified	78	0.35%	22	0.32%
Odontopyxis trispinosa	Pygmy Poacher	1	0.00%	0	0.00%
Ophiodon elongatus	Lingcod	27	0.12%	27	0.40%
Oxyjulis californica	Senorita	9	0.04%	0	0.00%
Oxylebius pictus	**Painted Greenling**	**321**	**1.45%**	**284**	**4.16%**
Phanerodon spp.	Surfperch	46	0.21%	6	0.09%
Phanerodon atripes	Sharpnose Seaperch	5	0.02%	1	0.01%
Phanerodon furcatus	White Seaperch	36	0.16%	0	0.00%
Pholidae	Gunnel	6	0.03%	4	0.06%
Raja binoculata	Big Skate	1	0.00%	0	0.00%
Rathbunella hypoplecta	Stripedfin Ronquil	7	0.03%	9	0.13%
Rhacochilus toxotes	Rubberlip Surfperch	7	0.03%	2	0.03%
Rhinogobiops nicholsii	**Blackeye Goby**	**3698**	**16.65%**	**1179**	**17.26%**
Scorpaena guttata	Striped Scorpionfish	1	0.00%	0	0.00%
Scorpaenichthys marmoratus	Cabezon	0	0.00%	1	0.01%
Sebastes atrovirens	Kelp Rockfish	2	0.01%	0	0.00%
Sebastes carnatus	**Gopher Rockfish**	139	0.63%	**144**	**2.11%**
Sebastes caurinus	Copper Rockfish	21	0.09%	21	0.31%
Sebastes chlorostictus	Greenspot Rockfish	27	0.12%	8	0.12%
Sebastes constellatus	**Starry Rockfish**	**256**	**1.15%**	51	0.75%
Sebastes emphaeus	Puget Rockfish	9	0.04%	2	0.03%
Sebastes ensifer	Swordspine Rockfish	7	0.03%	1	0.01%
Sebastes entomelas	**Widow Rockfish**	**362**	**1.63%**	**385**	**5.64%**
Sebastes flavidus	**Yellowtail Rockfish**	91	0.41%	**129**	**1.89%**
Sebastes helvomaculatus	Rosethorn Rockfish	1	0.00%	0	0.00%
Sebastes hopkinsi	**Squarespot Rockfish**	**1749**	**7.87%**	**1559**	**22.82%**
Sebastes jordani	Shortbelly Rockfish	1	0.00%	0	0.00%
Sebastes maliger	Quillback Rockfish	7	0.03%	0	0.00%
Sebastes melanops	Black Rockfish	0	0.00%	1	0.01%
Sebastes miniatus	**Vermilion Rockfish**	53	0.24%	**83**	**1.22%**
Sebastes moseri	Whitespeckeled Rockfish	0	0.00%	1	0.01%

Sebastes mystinus	**Blue Rockfish**	**501**	**2.26%**	**149**	**2.18%**
Sebastes nebulosus	China Rockfish	31	0.14%	8	0.12%
Sebastes ovalis	Speckled Rockfish	9	0.04%	4	0.06%
Sebastes paucispinis	Bocaccio	21	0.09%	4	0.06%
Sebastes pinniger	Canary Rockfish	41	0.18%	11	0.16%
Sebastes rosaceus	**Rosy Rockfish**	**1483**	**6.68%**	**726**	**10.63%**
Sebastes ruberrimus	Yelloweye Rockfish	3	0.01%	5	0.07%
Sebastes rufus	Bank Rockfish	10	0.05%	0	0.00%
Sebastes semicinctus	Halfbanded Rockfish	161	0.72%	7	0.10%
Sebastes serranoides	**Olive Rockfish**	**253**	**1.14%**	**168**	**2.46%**
Sebastes serriceps	Treefish	1	0.00%	1	0.01%
Sebastes spp	**Rockfish**	**6134**	**27.62%**	**1465**	**21.45%**
Sebastes wilsoni	**Pygmy Rockfish**	**6225**	**28.03%**	**76**	**1.11%**
Sebastes zacentrus	Sharpchin Rockfish	1	0.00%	0	0.00%
Sebastomus spp	**Sebastomus**	**221**	**1.00%**	**236**	**3.45%**
Stichaeidae	Prickleback	6	0.03%	0	0.00%
Torpedo Californica	Pacific Electric Ray	1	0.00%	0	0.00%
Zalembius rosaceus	Pink Surfperch	9	0.04%	0	0.00%
Zaniolepis frenata	Shortspine Combfish	6	0.03%	0	0.00%

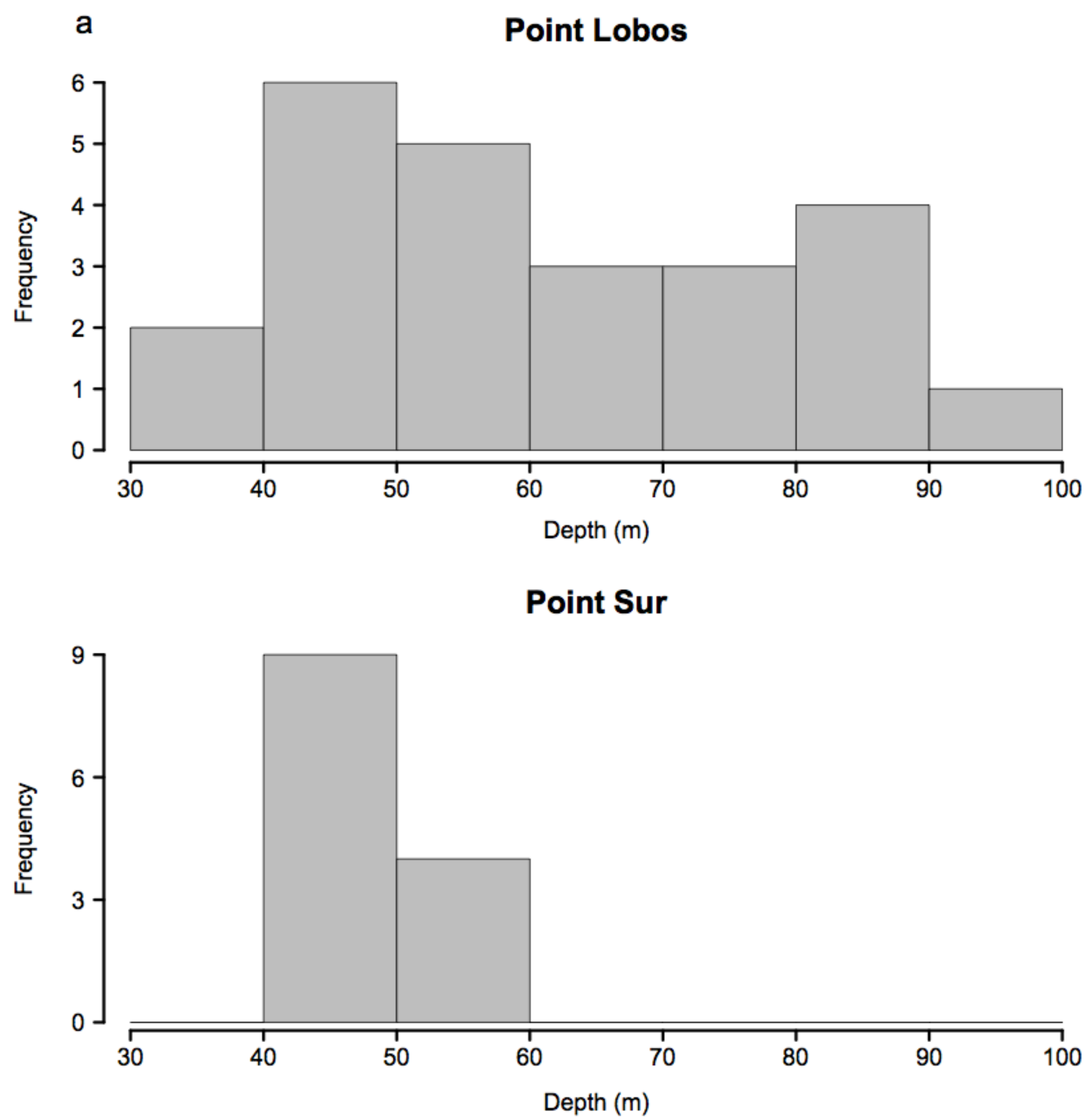
Appendix B Length-weight parameters obtained from published, peer-reviewed literature that were used during this study. The listed units are from the original publication. Sources of each parameter, or the proxy species used, are listed

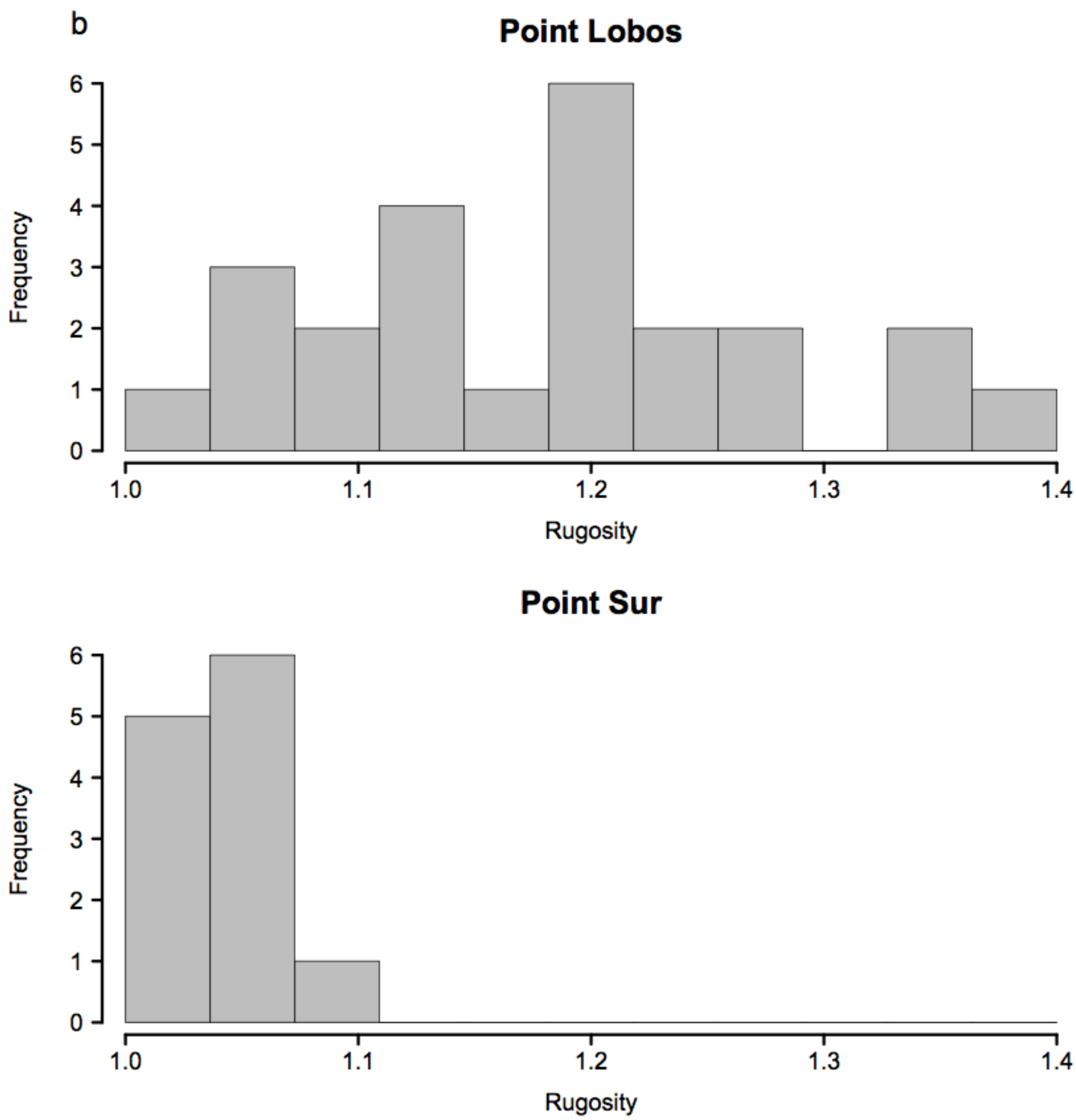
Scientific Names	Common Names	a	b	units	Sources
Agonidae	Poacher	0.003	3.206	g/cm	Glubokov & Orlov 2007 (*Percis japonica* , *Sarritor frenatus*)
Anarrhichthys ocellatus	Wolf Eel	0.050	3.091	kg/mm	Karpov 1986
Citharichthys sordidus	Sanddab	0.000	3.260	g/mm	Rackowski& Pikitch 1989
Cottidae	Sculpin	0.055	3.160	g/mm	Stokley 1952
Damalichthys vacca	Pile Surfperch	0.000	3.135	g/mm	DeMartini et al. 1994
Embiotoca jacksoni	Black Surfperch	0.001	2.864	g/mm	Froeschke et al 2007
Embiotoca lateralis	Striped Surfperch	0.154	3.010	kg/mm	Karpov 1986
Hexagrammos decagrammus	Kelp Greenling	0.016	3.000	g/cm	Fishbase
Hydrolagus colliei	Ratfish	0.002	2.755	kg/mm	Barnet 2008
Icelinus tenuis	Spotfin Sculpin	0.179	2.896	kg/mm	Karpov 1986
Microstomus pacificus	Dover Sole	0.002	3.436	g/cm	NOAA-TM-AFSC-89
Pleuronectiformes	Flatfishes	0.004	3.223	g/cm	NOAA-TM-AFSC-89
Odontopyxis trispinosa	Pygmy Poacher	0.003	3.206	g/cm	Glubokov & Orlov 2007
Ophiodon elongatus	Lingcod	0.002	3.390	g/cm	Pikitch & Rogers 1989
Oxyjulis californica	Senorita	0.000	3.500	g/mm (SL)	Eschmeyer 1998
Oxylebius pictus	Painted Greenling	0.032	3.384	g/mm	deMartini & Anderson
Phanerodon spp.	Surfperch	0.100	3.192	kg/mm	Karpov 1986
Phanerodon atripes	Sharpnose Seaperch	0.100	3.192	kg/mm	Karpov 1986
Phanerodon furcatus	White Seaperch	0.001	2.996	g/mm	Quast 1968b; Antrim 1981
Pholidae	Gunnel	0.007	3.249	g/cm	Fishbase
Raja binoculata	Big Skate	0.050	3.106	kg/mm	Ebert et al. 2008
Raja rhina	Longnose Skate	0.060	3.091	kg/mm	Ebert et al. 2008
Raja spp.	Skates	0.004	3.181	g/cm	Moutopoulos & Stergiou 2002 (*Raja miraletus* , *Raja radula*)
Rathbunella hypoplecta	Stripedfin Ronquil	NA	NA	NA	NA
Rhacochilus toxotes	Rubberlip Surfperch	0.000	3.360	g/mm (SL)	Quast 1968b
Rhamphocottus richardsonii	Grunt Sculpin	0.179	2.896	kg/mm	Karpov 1986
Rhinogobiops nicholsii	Blackeye Goby	0.000	3.470	mg/mm	Mesa 1999 (*Aphia minuta* , *Crystallogobius linearis*)
Scorpaena guttata	Striped Scorpionfish	0.020	3.007	g/cm	Love et al 1987
Scorpaenichthys marmoratus	Cabezon	0.029	3.000	g/cm	Fishbase
Sebastes atrovirens	Kelp Rockfish	0.000	3.172	g/mm	Lea et al. 1999
Sebastes carnatus	Gopher Rockfish	0.027	3.000	g/cm	Fishbase
Sebastes caurinus	Copper Rockfish	0.018	3.040	g/cm	Fishbase; Haldstorm & Love 1991
Sebastes chlorostictus	Greenspot Rockfish	0.000	3.001	g/mm	Love 1987
Sebastes constellatus	Starry Rockfish	0.016	3.160	g/cm	Fishbase; Haldstorm & Love 1991
Sebastes elongatus	Greenstripe Rockfish	0.008	3.144	g/cm	NOAA-TM-AFSC-89
Sebastes emphaeus	Puget Rockfish	0.059	2.687	g/cm	Fishbase
Sebastes ensifer	Swordspine Rockfish	0.013	2.970	g/cm	Love 1987
Sebastes entomelas	Widow Rockfish	0.005	3.341	g/cm	Pikitch & Rogers 1989
Sebastes flavidus	Yellowtail Rockfish	0.013	3.055	g/cm	Pikitch & Rogers 1989
Sebastes helvomaculatus	Rosethorn Rockfish	0.010	3.119	g/cm	NOAA-TM-AFSC-89
Sebastes hopkinsi	Squarespot Rockfish	0.015	2.964	g/cm	Love 1987
Sebastes jordani	Shortbelly Rockfish	0.014	3.152	NA	NA
Sebastes levis	Cowcod	0.014	3.093	g/cm	Fishbase; Haldstorm & Love 1991
Sebastes maliger	Quillback Rockfish	0.030	3.000	g/cm	Fishbase
Sebastes melanops	Black Rockfish	0.021	3.286	g/cm	Fishbase; Haldstorm & Love 1991
Sebastes miniatus	Vermilion Rockfish	0.033	2.923	g/cm	Fishbase; Haldstorm & Love 1991
Sebastes moseri	Whitespeckeled Rockfis	0.014	3.152	NA	NA
Sebastes mystinus	Blue Rockfish	0.017	2.808	g/cm	Fishbase; Haldstorm & Love 1991
Sebastes nebulosus	China Rockfish	0.023	3.000	g/cm	Fishbase
Sebastes ovalis	Speckled Rockfish	0.006	3.177	g/cm	Love 1987
Sebastes paucispinis	Bocaccio	0.008	3.199	g/cm	Pikitch & Rogers 1989
Sebastes pinniger	Canary Rockfish	0.012	3.107	g/cm	Pikitch & Rogers 1989
Sebastes rosaceus	Rosy Rockfish	0.005	3.386	g/cm	Love 1987
Sebastes ruberrimus	Yelloweye Rockfish	0.014	3.000	g/cm	Fishbase
Sebastes rubrivinctus	Flag Rockfish	0.015	3.000	g/cm	Fishbase
Sebastes rufus	Bank Rockfish	0.015	3.147	g/cm	Fishbase; Haldstorm & Love 1991
Sebastes semicinctus	Halfbanded Rockfish	0.014	2.977	g/cm	Haldstorm & Love 1991
Sebastes serranoides	Olive Rockfish	0.011	2.968	g/cm	Fishbase
Sebastes serriceps	Treefish	0.005	3.341	g/cm	Pikitch & Rogers 1989
Sebastes spp.	Rockfish	0.014	3.154	NA	NA
Sebastes wilsoni	Pygmy Rockfish	0.014	3.154	NA	NA
Sebastes zacentrus	Sharpchin Rockfish	0.006	3.282	g/cm	NOAA-TM-AFSC-89
Sebastomus spp.	Sebastomus	0.000	3.293	g/mm	Rogers at al 1998, Ianelli et al. 1994, Miller 1985
Stichaeidae	Prickleback	0.024	3.303	g/cm	LeDrew & Green 1975
Torpedo Californica	Pacific Electric Ray	0.030	2.948	g/mm	Neer & Cailliet 2001
Zalembius rosaceus	Pink Surfperch	0.100	3.192	kg/mm	Karpov 1986
Zaniolepis frenata	Shortspine Combfish	0.003	3.323	g/cm	Rodriguez-Romero et al 2009 (*Zaniolepis latipinnis*)
Zaniolepis spp.	Combfish	0.003	3.323	g/cm	Rodriguez-Romero et al 2009 (*Zaniolepis latipinnis*)

Appendix C Equations and definitions of the diversity variables used in species composition calculations

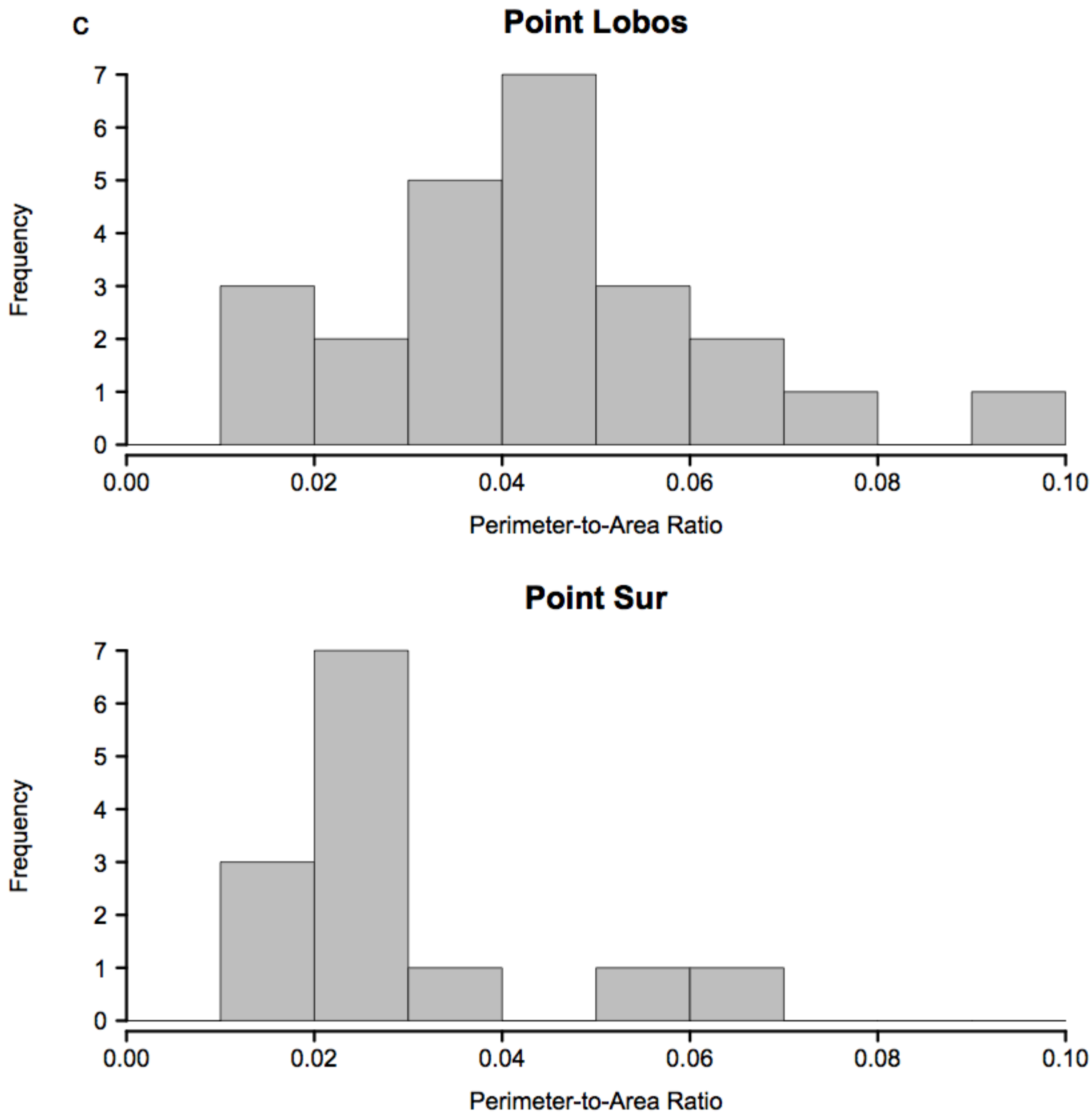
	Equation	Variables
Bray-Curtis Index of Similarity	$$BC_{ij} = \frac{S_i + S_j - 2C_{ij}}{S_i + S_j}$$	C_{ij} - sum of minimum abundance of the various species S_i - total number of individuals in sample i S_j - total number of individuals in sample j
Heterogeneity (Shannon-Weiner)	$$H' = -\sum_{i=1}^{S} p_i * ln\left(p_i\right)$$	n_i - number of individuals in species i S - number of species (richness) N - total number of all individuals p_i - relative abundance of each species
Evenness (Pielou)	$$E = \frac{H'}{H_{max}}$$	H' - species heterogeneity H max - maximum value of H': $$H_{max} = -\sum_{i=1}^{S} \frac{1}{S} * ln\left(\frac{1}{S}\right) = ln\left(S\right)$$

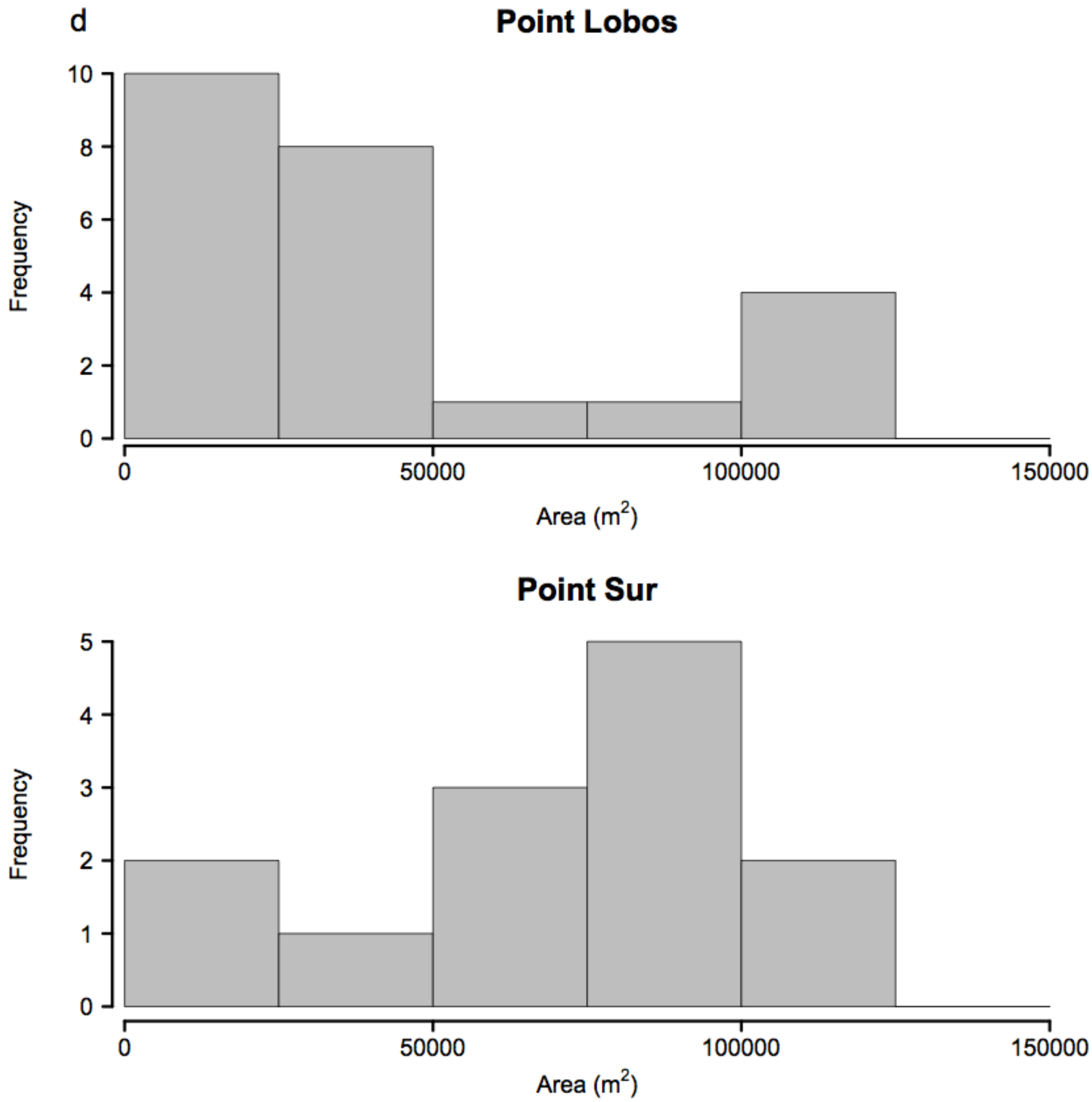
Appendix D Frequency histograms of the independent habitat variables per rocky bank patch near Point Lobos and Point Sur. The mean depth (a), rugosity (b), P:A ratio (c), and area (d) per patch near Point Lobos (n = 24) and near Point Sur (n = 13)




b
Point Lobos
Frequency
0
1
2
3
4
5
6
1.0
1.1
1.2
1.3
1.4
Rugosity
Point Sur
Frequency
0
1
2
3
4
5
6
1.0
1.1
1.2
1.3
1.4
Rugosity

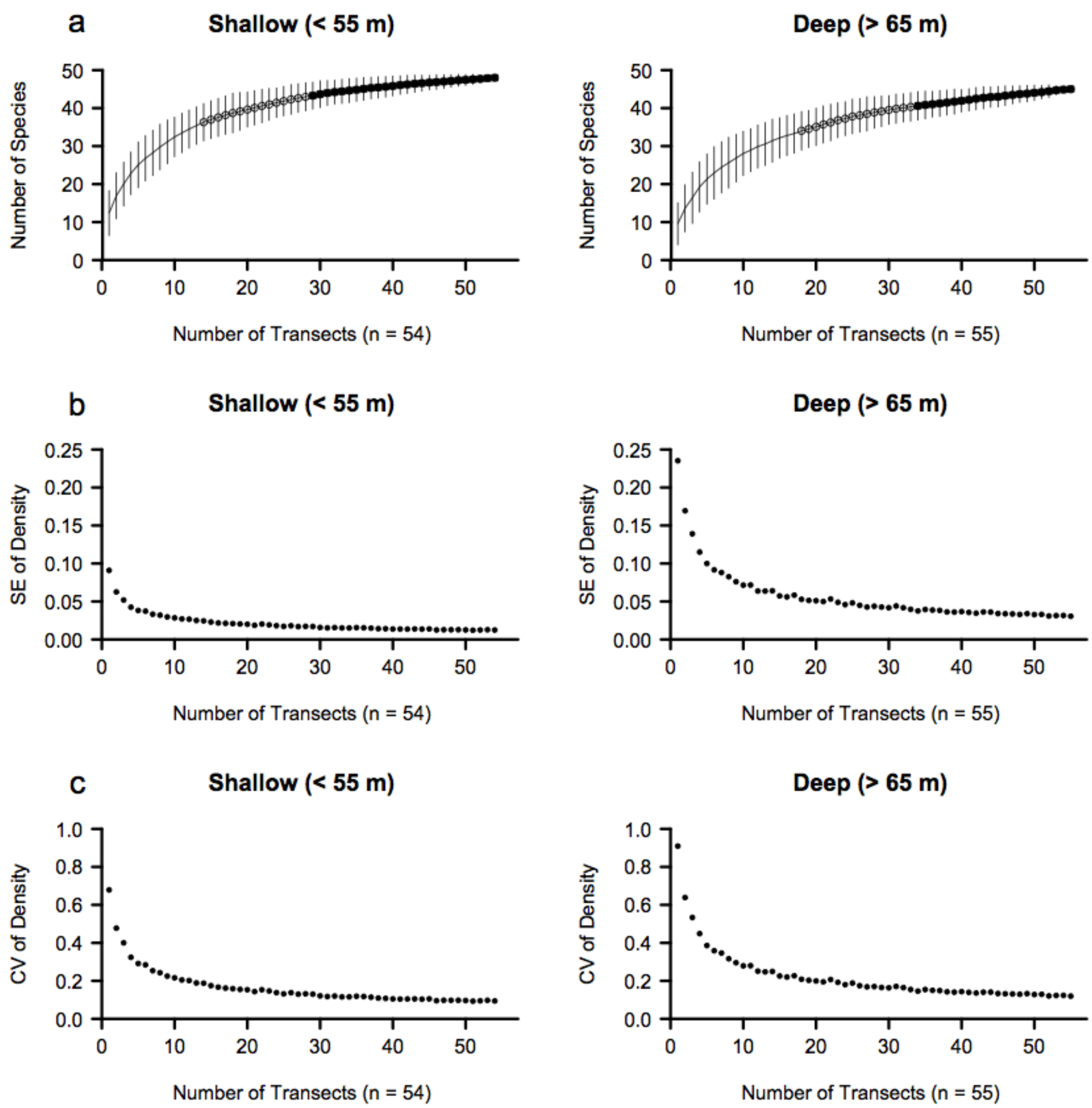
c


Point Lobos
Frequency
0
1
2
3
4
5
6
7
0.00
0.02
0.04
0.06
0.08
0.10
Perimeter-to-Area Ratio
Point Sur
Frequency
0
1
2
3
4
5
6
7
0.00
0.02
0.04
0.06
0.08
0.10
Perimeter-to-Area Ratio


d
Point Lobos
Frequency
10
8
6
4
2
0
0
50000
100000
150000
Area (m2)
Point Sur
Frequency
5
4
3
2
1
0
0
50000
100000
150000
Area (m2)

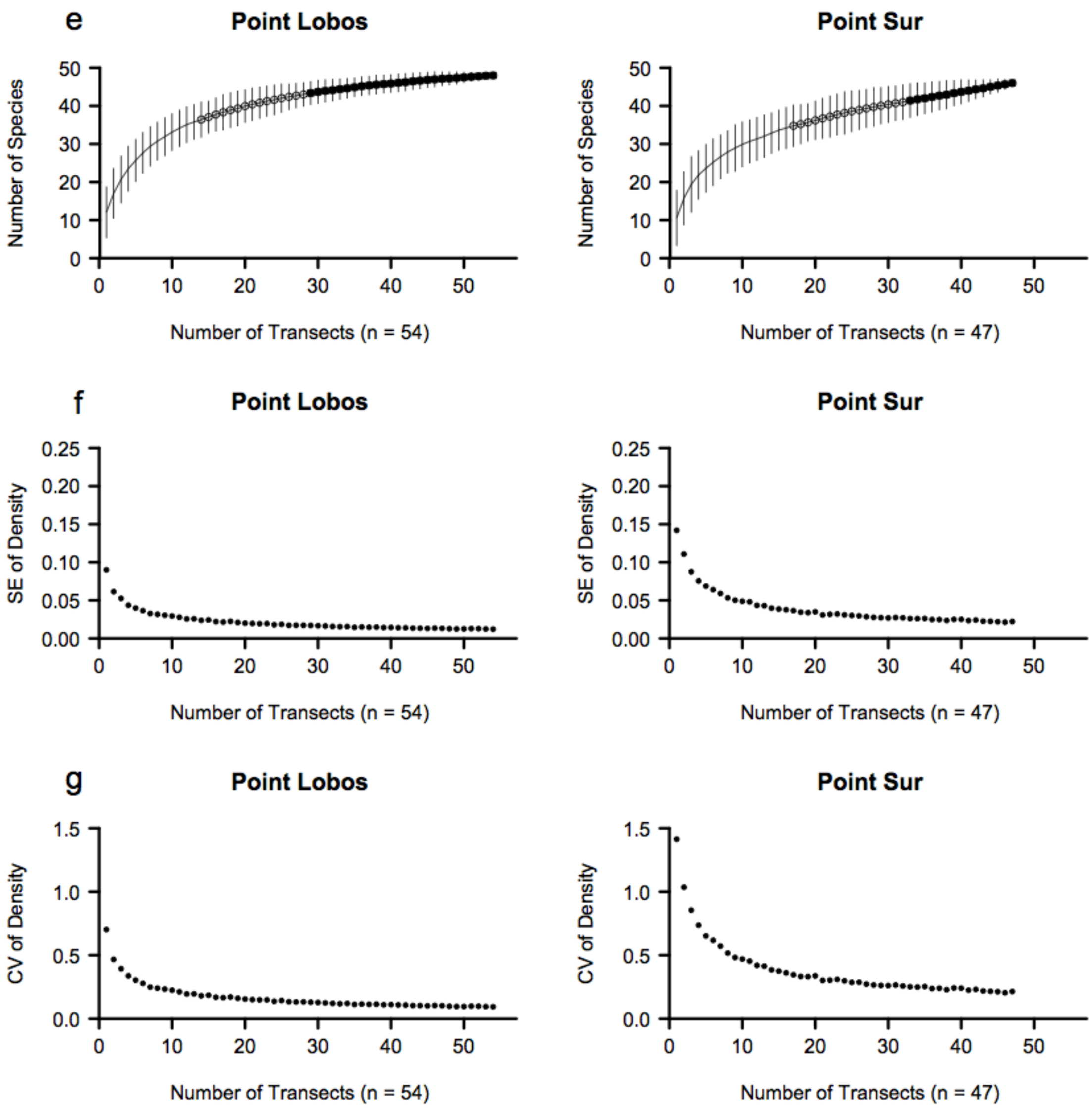
Appendix E Species-accumulation curves and comparisons of standard error and coefficient of variation of density. The results are reported for species richness with depth (a) and comparisons of standard error and coefficient of variation of density for shallow and deep rocky bank patches (b-c) near Point Lobos (1) and shallow depths near Point Lobos and Point Sur (2 e-g). The slope through the final four points, to determine if an asymptote was reached, are included in the tables for near Point Lobos (1 d) and near Point Sur (2 h). Open circles denote 75% of the total number of species observed and filled circles denote 90% of the total number of species observed

1) Point Lobos shallow and deep



d	Shallow		Deep	
Index	**Slope**	**Asymptote?**	**Slope**	**Asymptote?**
Richness	0.173	No	0.140	No
Standard Error (Density)	< -0.001	Yes	< -0.001	Yes
Coefficient of Variation (Density)	< -0.001	Yes	-0.001	Yes

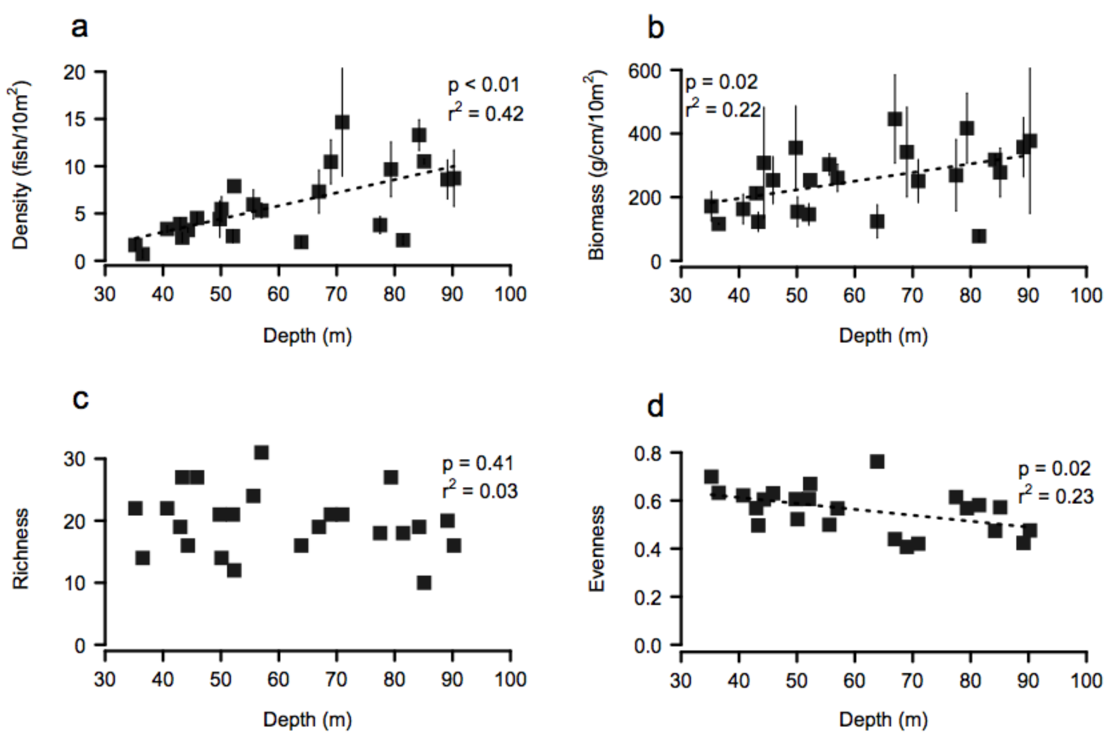
2) Point Lobos and Point Sur (shallow)

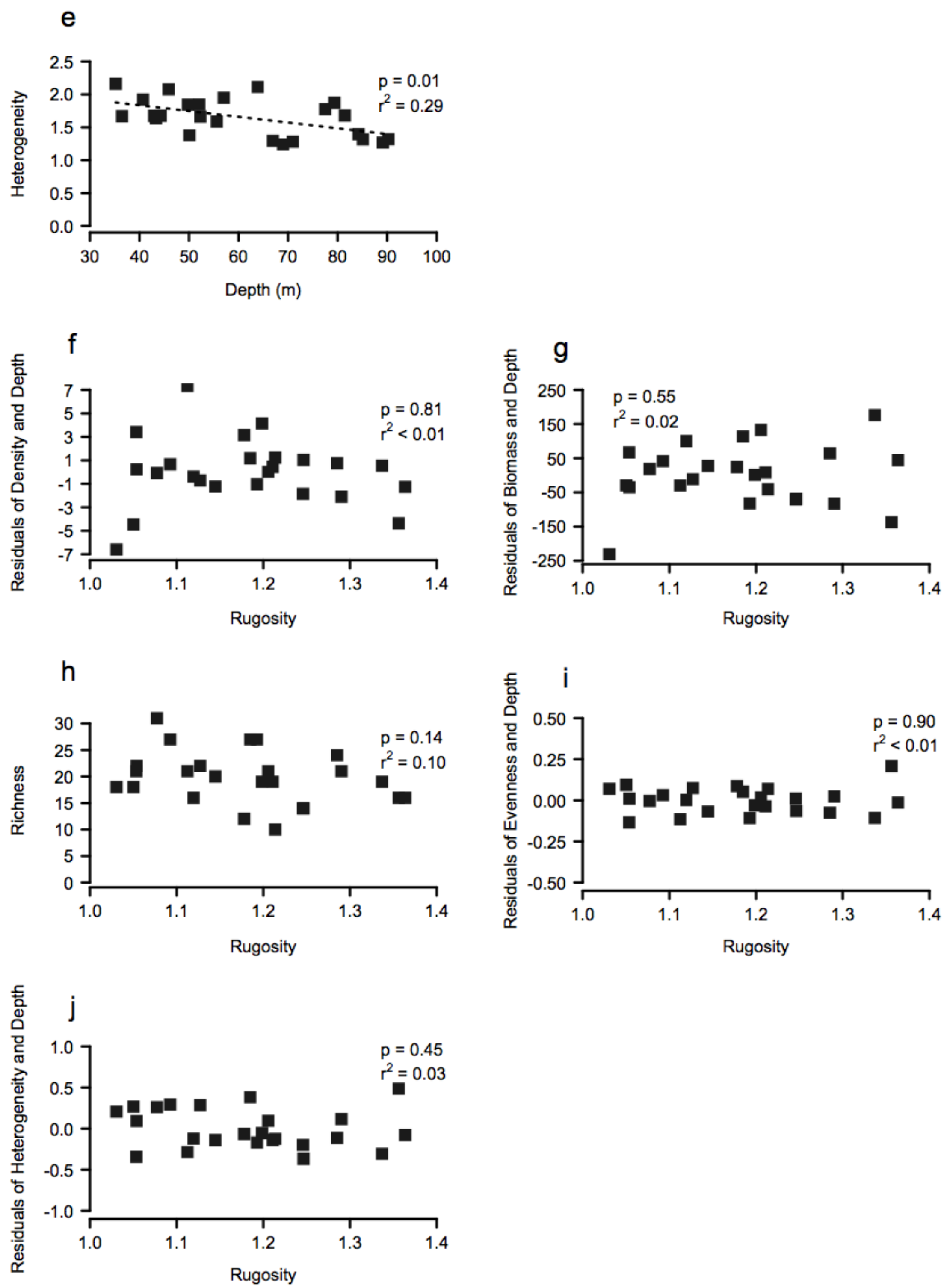


h	Point Lobos		Point Sur	
Index	**Slope**	**Asymptote?**	**Slope**	**Asymptote?**
Richness	0.130	No	0.240	No
Standard Error (Density)	< 0.001	Yes	< -0.001	Yes
Coefficient of Variation (Density)	< 0.001	Yes	-0.002	Yes

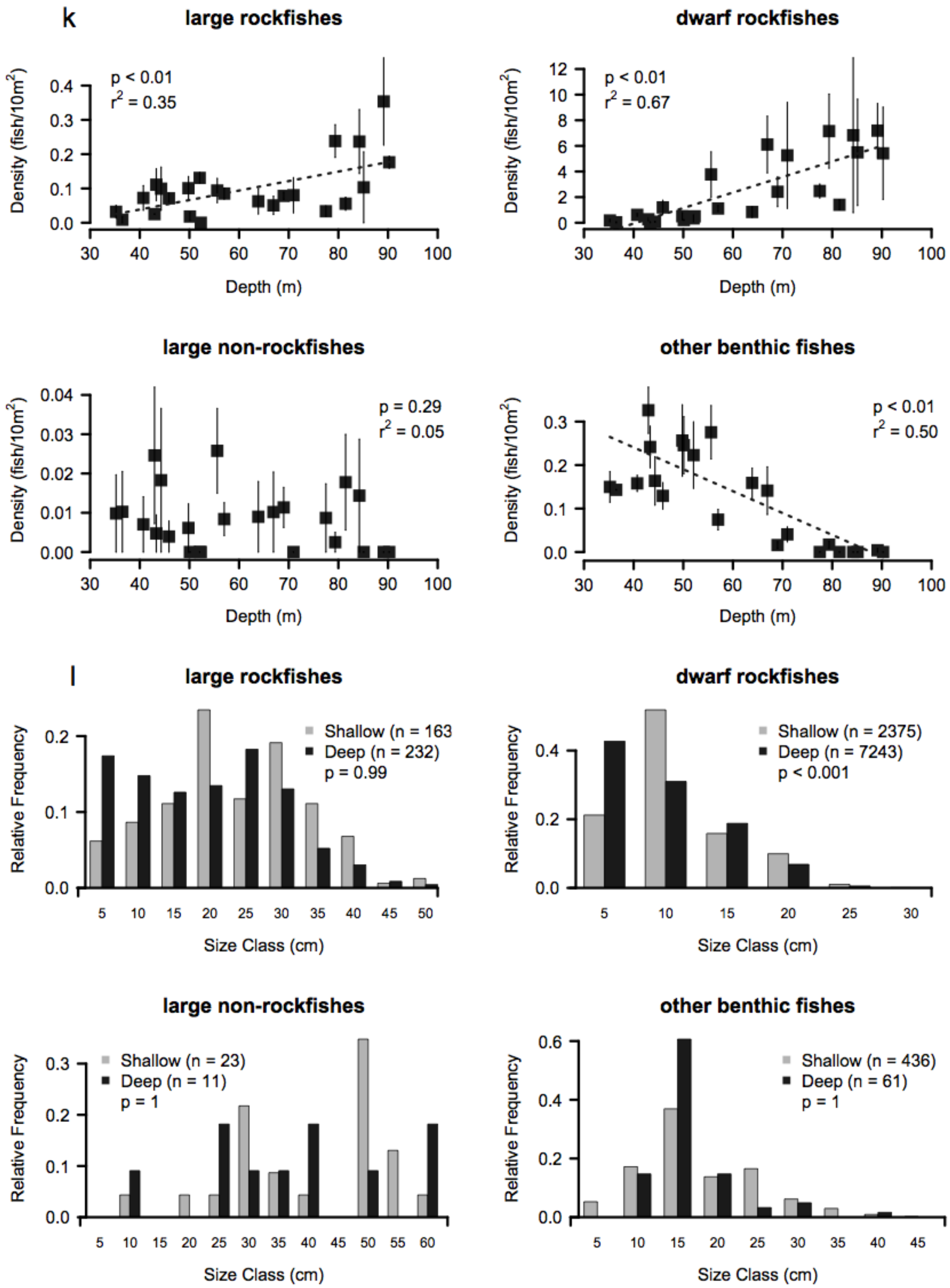
Appendix F Biological response variables of nearshore fish assemblage with respect to depth and rugosity near Point Lobos. These results are grouped by the (1) assemblage, (2) species groups, and (3) the species-specific analyses. Assemblage relationships of density (a), biomass (b), richness (c), evenness (d), and heterogeneity (e) with respect to depth are reported. In addition, the relationships among rugosity with the assemblage density (f), biomass (g), richness (h), evenness (i), and heterogeneity (j) are reported. Species-group relationships for the density (k) and length distributions (l) with respect to depth and rugosity (respectively, m-n) are reported. Species-specific relationships of density (o), biomass (p), mean length (q), and length distributions (r) with respect to depth are reported. Species-specific relationships among rugosity with respect to density (s), biomass (t), mean length (u), and length distributions (v) are reported. Gray denotes the shallow depth category and black denotes the deep depth category. Asterisks indicate size classes in which fish were observed in abundances too small to be observed on the relative frequency histograms. Standard error is plotted as vertical bars. Significant linear relationships are denoted with dashed regression lines. P-values, and when applicable, r^2 values are included in the legends

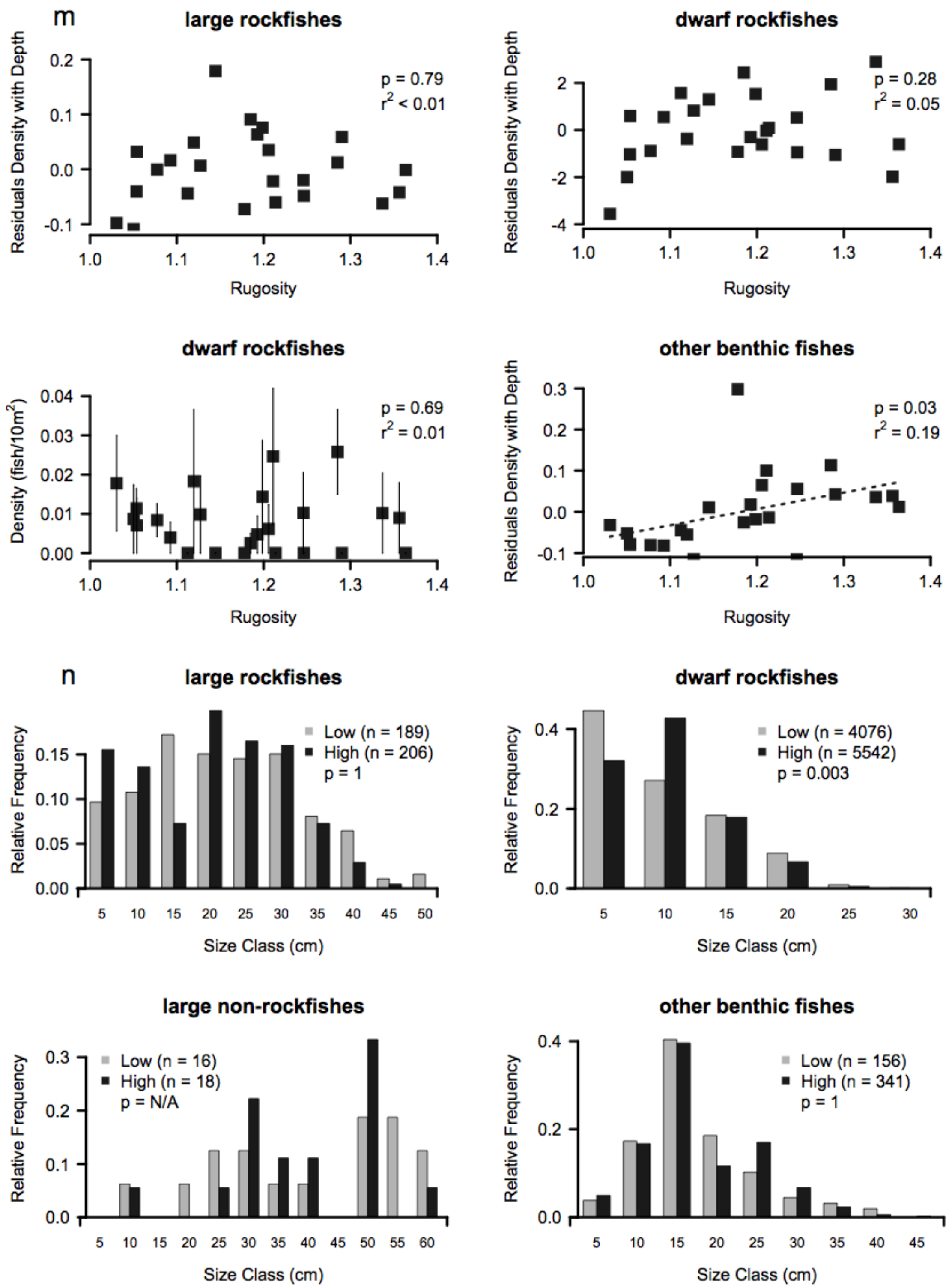
1. Assemblage



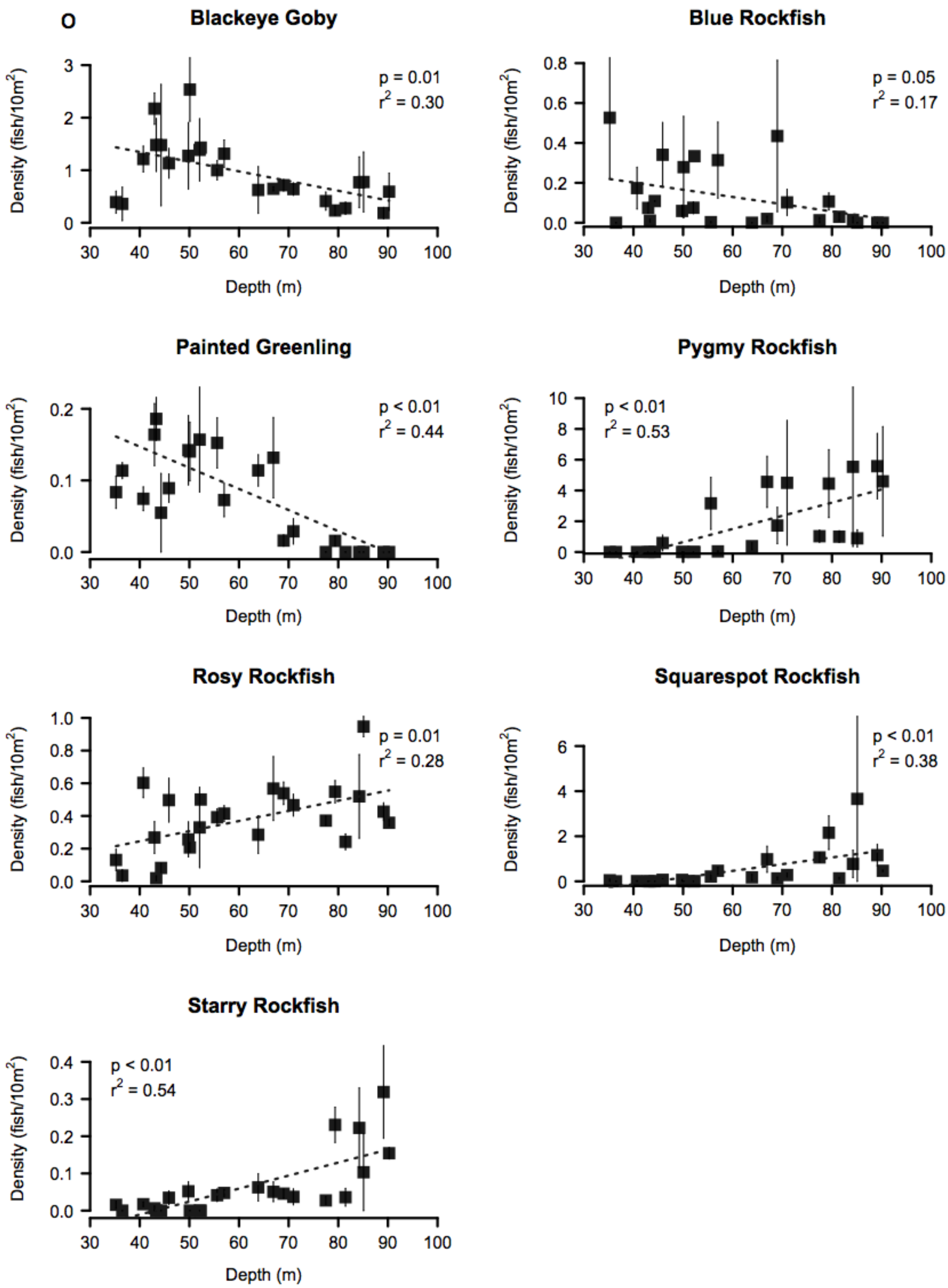


2. Species groups

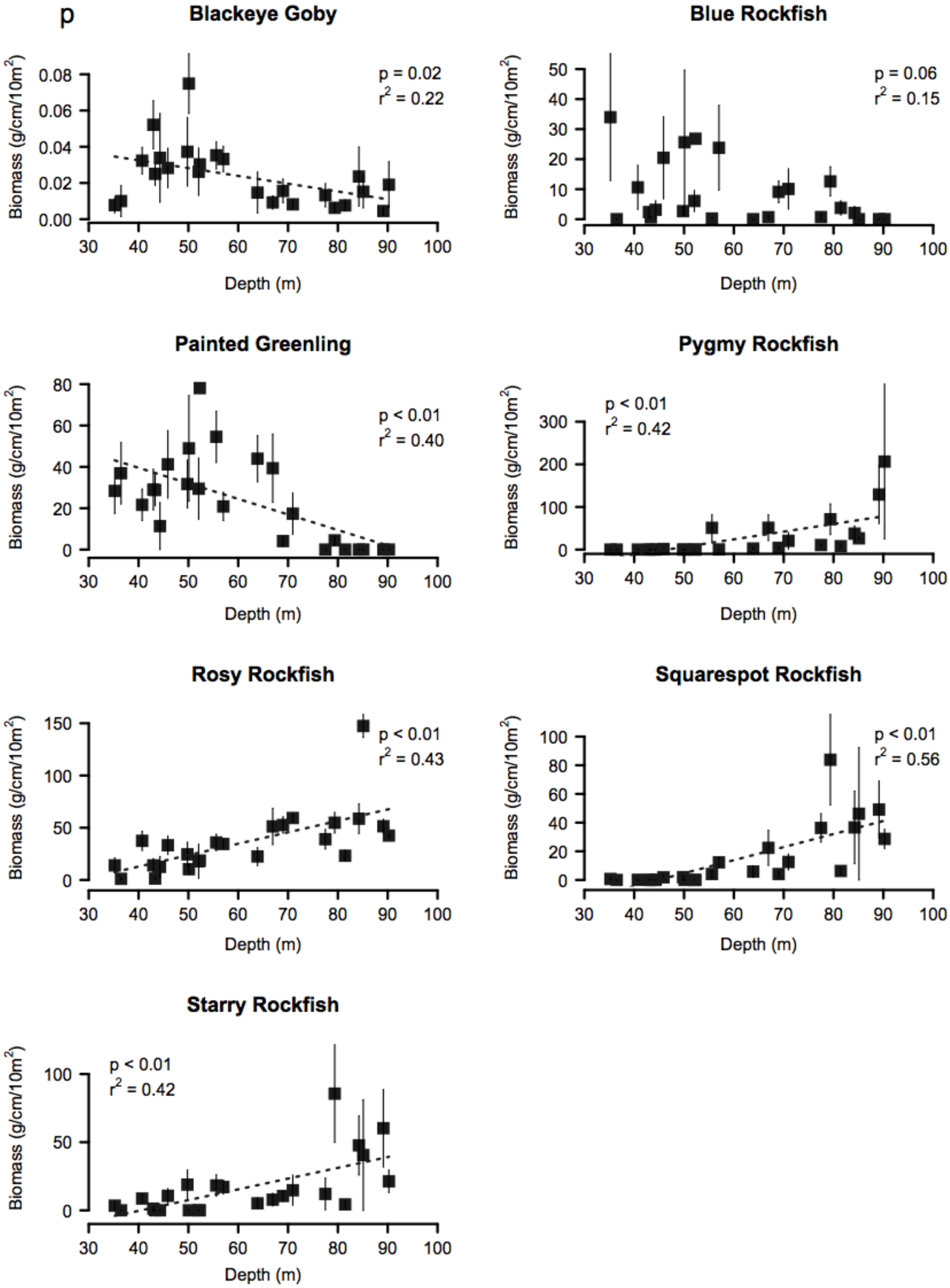

k
large rockfishes
p < 0.01
r2 = 0.35
Density (fish/10m2)
Depth (m)
dwarf rockfishes
p < 0.01
r2 = 0.67
large non-rockfishes
p = 0.29
r2 = 0.05
other benthic fishes
p < 0.01
r2 = 0.50
l
large rockfishes
Shallow (n = 163
Deep (n = 232)
p = 0.99
Relative Frequency
Size Class (cm)
dwarf rockfishes
Shallow (n = 2375)
Deep (n = 7243)
p < 0.001
large non-rockfishes
Shallow (n = 23)
Deep (n = 11)
p = 1
other benthic fishes
Shallow (n = 436)
Deep (n = 61)
p = 1

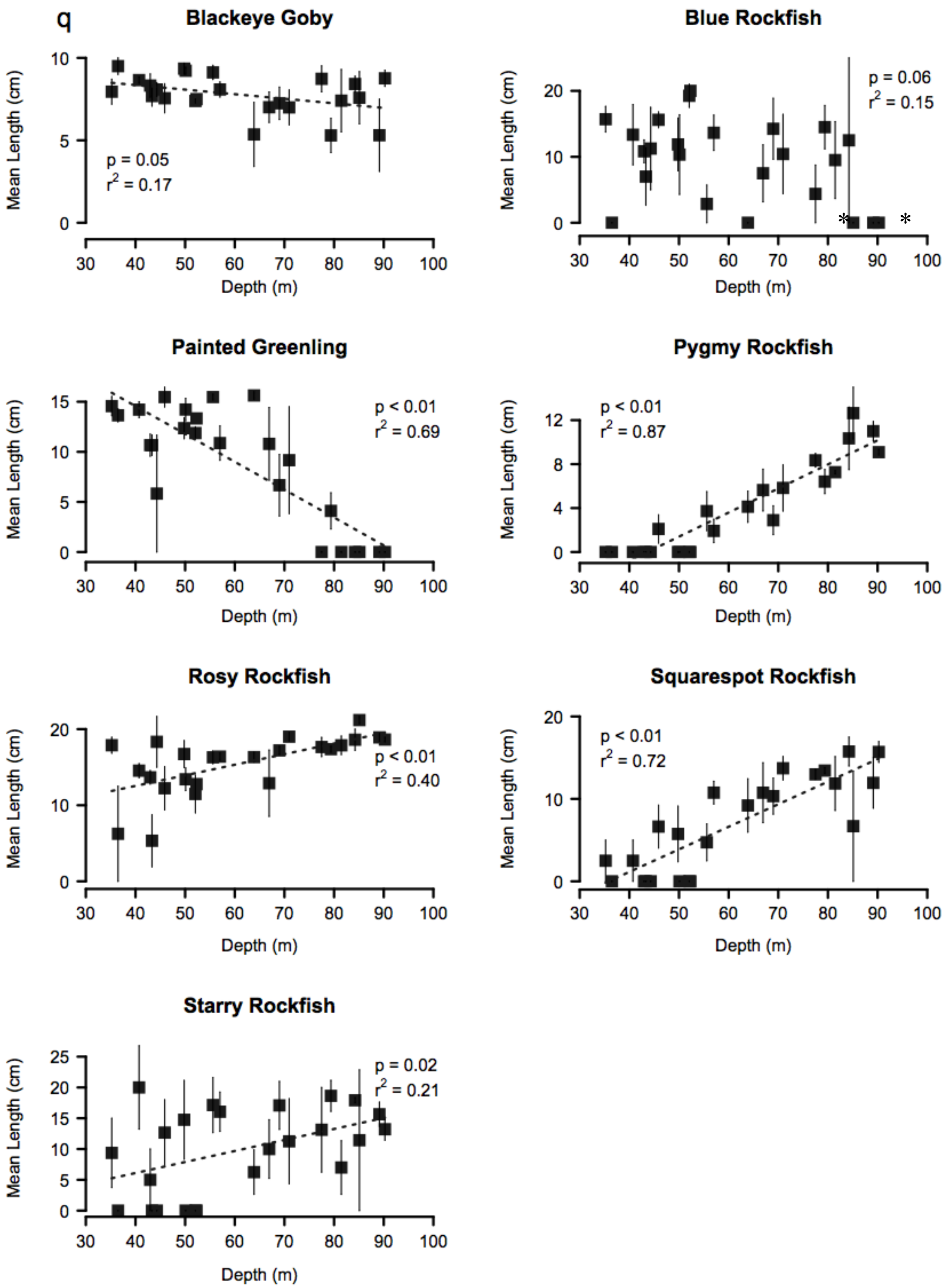


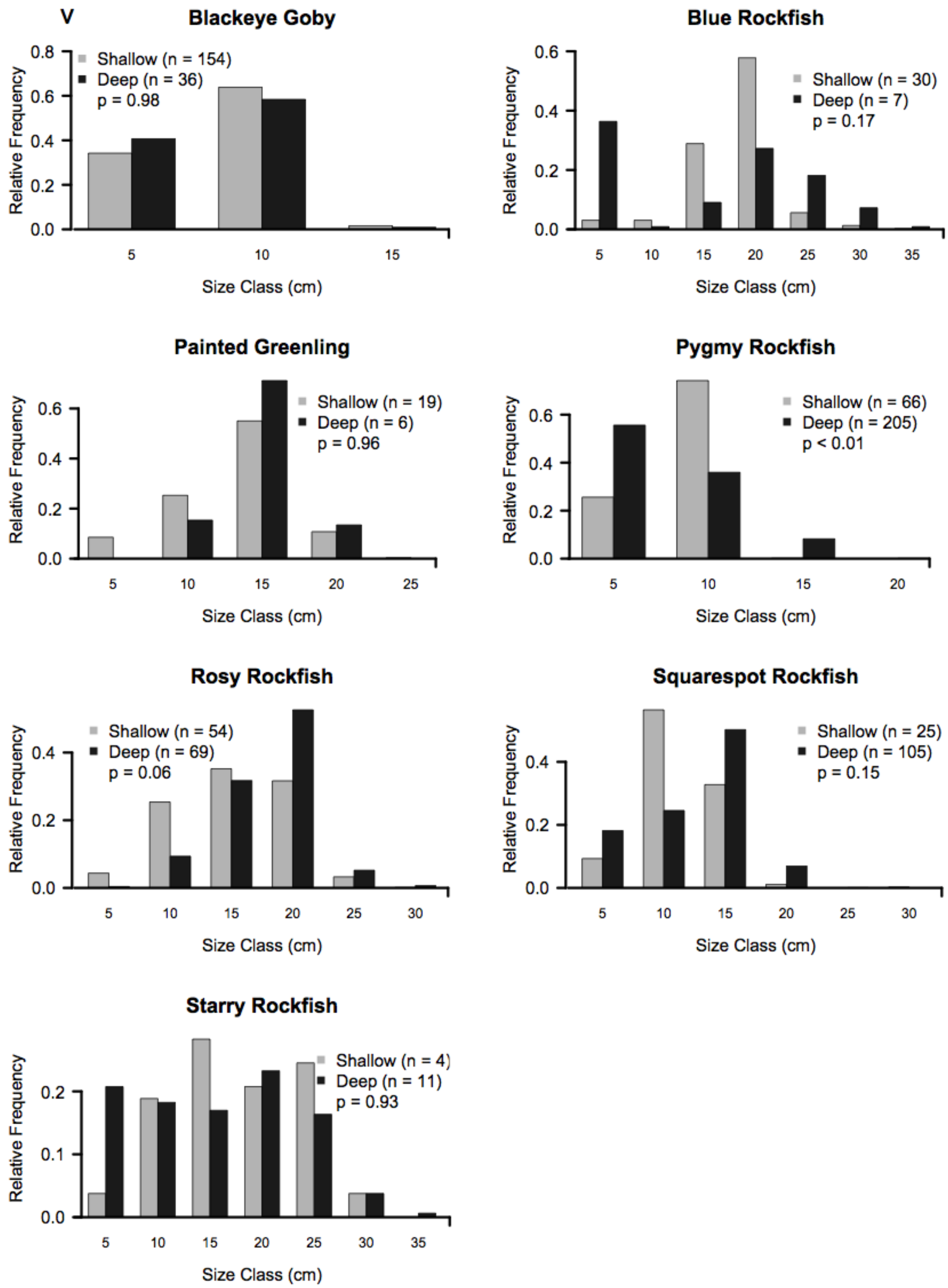
3. Specific species

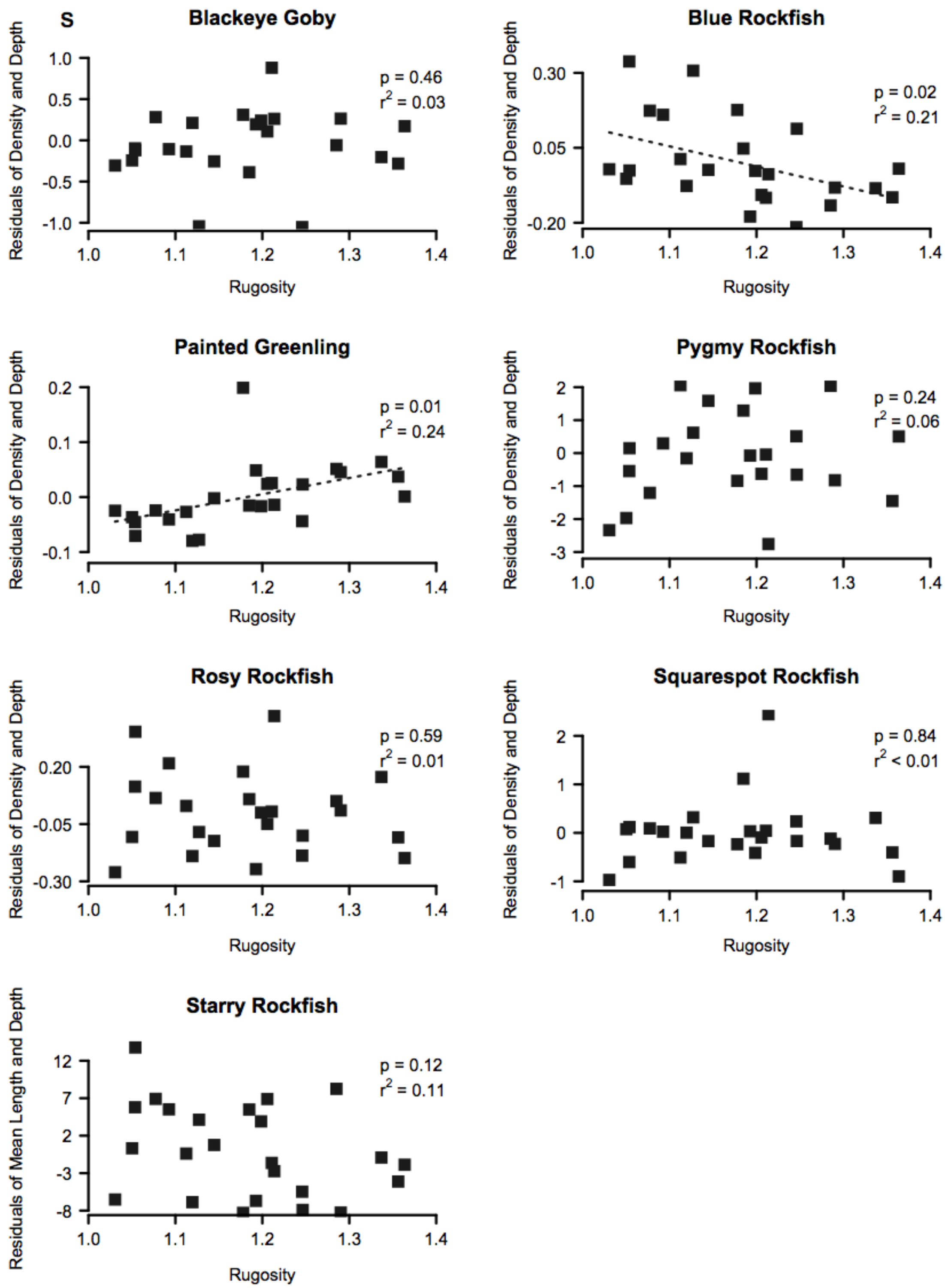

O
Blackeye Goby
p = 0.01
r2 = 0.30
Blue Rockfish
p = 0.05
r2 = 0.17
Painted Greenling
p < 0.01
r2 = 0.44
Pygmy Rockfish
p < 0.01
r2 = 0.53
Rosy Rockfish
p = 0.01
r2 = 0.28
Squarespot Rockfish
p < 0.01
r2 = 0.38
Starry Rockfish
p < 0.01
r2 = 0.54
Density (fish/10m2)
Depth (m)

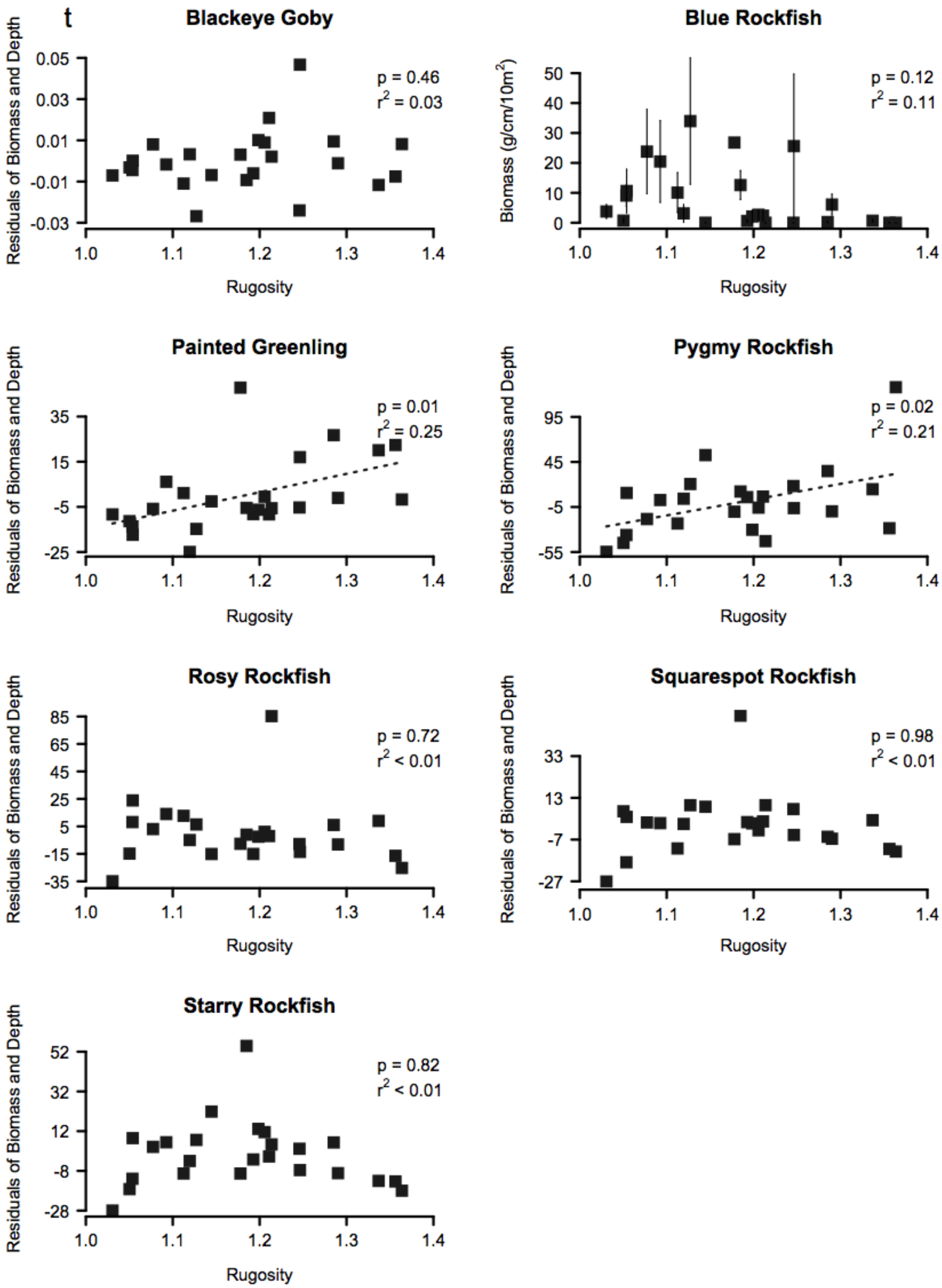
p


Blackeye Goby
p = 0.02
r^2 = 0.22
Blue Rockfish
p = 0.06
r^2 = 0.15
Painted Greenling
p < 0.01
r^2 = 0.40
Pygmy Rockfish
p < 0.01
r^2 = 0.42
Rosy Rockfish
p < 0.01
r^2 = 0.43
Squarespot Rockfish
p < 0.01
r^2 = 0.56
Starry Rockfish
p < 0.01
r^2 = 0.42
Biomass (g/cm/10m^2)
Depth (m)

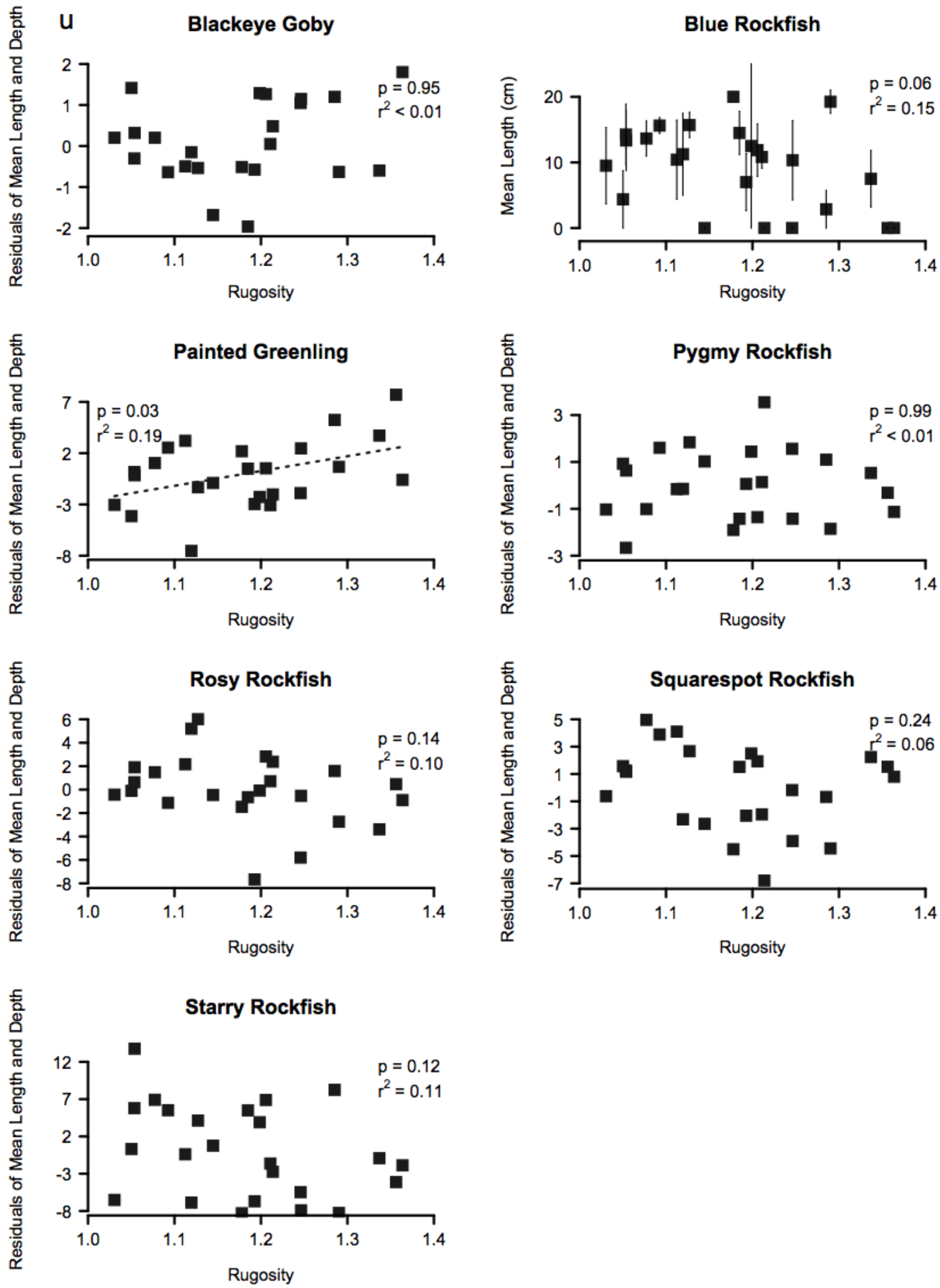

q
Blackeye Goby
Mean Length (cm)
Depth (m)
p = 0.05
r2 = 0.17
Blue Rockfish
Mean Length (cm)
Depth (m)
p = 0.06
r2 = 0.15
*
*
Painted Greenling
Mean Length (cm)
Depth (m)
p < 0.01
r2 = 0.69
Pygmy Rockfish
Mean Length (cm)
Depth (m)
p < 0.01
r2 = 0.87
Rosy Rockfish
Mean Length (cm)
Depth (m)
p < 0.01
r2 = 0.40
Squarespot Rockfish
Mean Length (cm)
Depth (m)
p < 0.01
r2 = 0.72
Starry Rockfish
Mean Length (cm)
Depth (m)
p = 0.02
r2 = 0.21

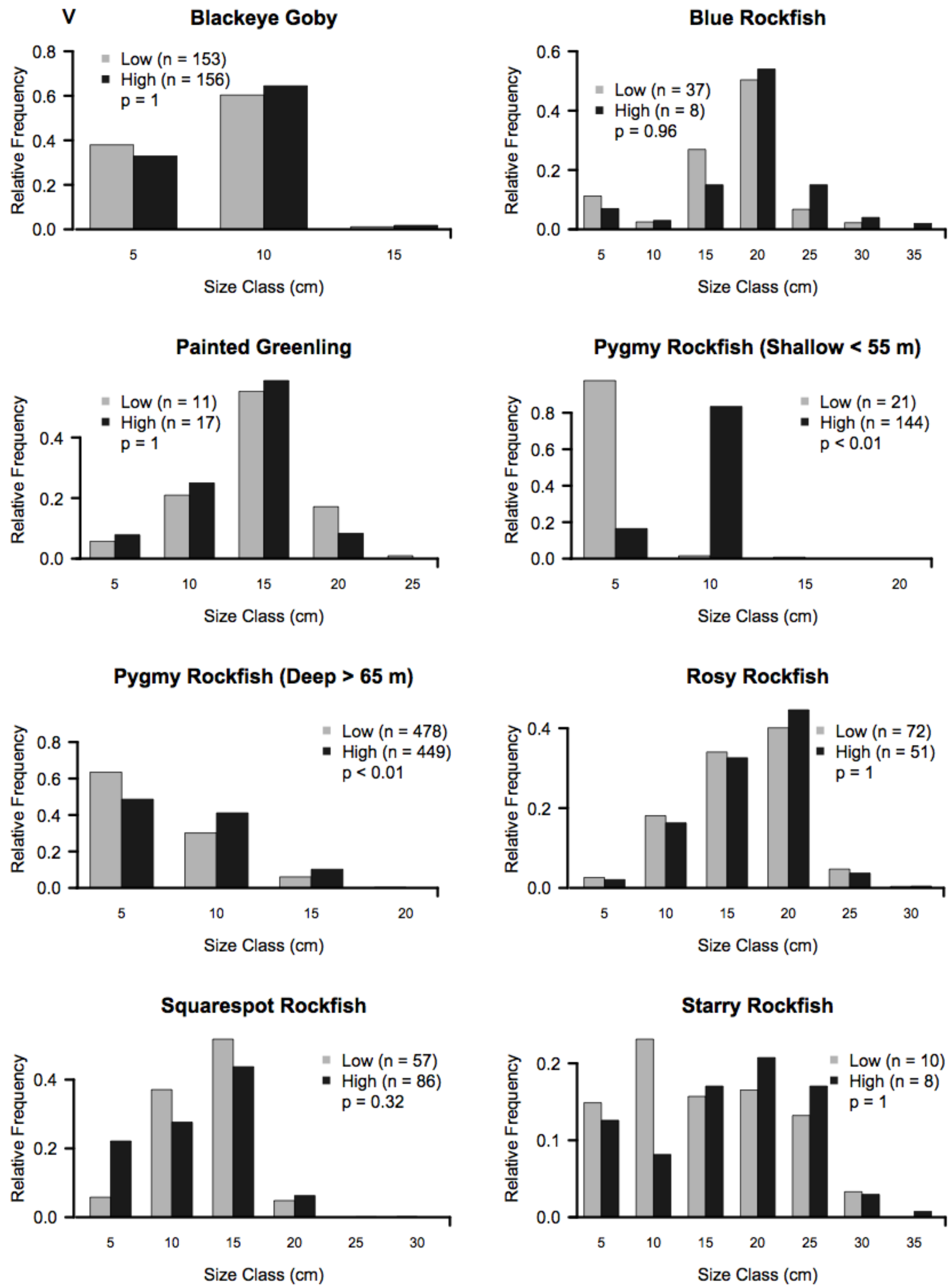

V
Blackeye Goby
Shallow (n = 154)
Deep (n = 36)
p = 0.98
Relative Frequency
Size Class (cm)
Blue Rockfish
Shallow (n = 30)
Deep (n = 7)
p = 0.17
Painted Greenling
Shallow (n = 19)
Deep (n = 6)
p = 0.96
Pygmy Rockfish
Shallow (n = 66)
Deep (n = 205)
p < 0.01
Rosy Rockfish
Shallow (n = 54)
Deep (n = 69)
p = 0.06
Squarespot Rockfish
Shallow (n = 25)
Deep (n = 105)
p = 0.15
Starry Rockfish
Shallow (n = 4)
Deep (n = 11)
p = 0.93


S
Blackeye Goby
p = 0.46
r2 = 0.03
Residuals of Density and Depth
Rugosity
Blue Rockfish
p = 0.02
r2 = 0.21
Residuals of Density and Depth
Rugosity
Painted Greenling
p = 0.01
r2 = 0.24
Residuals of Density and Depth
Rugosity
Pygmy Rockfish
p = 0.24
r2 = 0.06
Residuals of Density and Depth
Rugosity
Rosy Rockfish
p = 0.59
r2 = 0.01
Residuals of Density and Depth
Rugosity
Squarespot Rockfish
p = 0.84
r2 < 0.01
Residuals of Density and Depth
Rugosity
Starry Rockfish
p = 0.12
r2 = 0.11
Residuals of Mean Length and Depth
Rugosity



t
Blackeye Goby
p = 0.46
r^2 = 0.03
Residuals of Biomass and Depth
Rugosity
Blue Rockfish
p = 0.12
r^2 = 0.11
Biomass (g/cm/10m^2)
Rugosity
Painted Greenling
p = 0.01
r^2 = 0.25
Residuals of Biomass and Depth
Rugosity
Pygmy Rockfish
p = 0.02
r^2 = 0.21
Residuals of Biomass and Depth
Rugosity
Rosy Rockfish
p = 0.72
r^2 < 0.01
Residuals of Biomass and Depth
Rugosity
Squarespot Rockfish
p = 0.98
r^2 < 0.01
Residuals of Biomass and Depth
Rugosity
Starry Rockfish
p = 0.82
r^2 < 0.01
Residuals of Biomass and Depth
Rugosity


U
Blackeye Goby
p = 0.95
r2 < 0.01
Residuals of Mean Length and Depth
Rugosity
Blue Rockfish
p = 0.06
r2 = 0.15
Mean Length (cm)
Rugosity
Painted Greenling
p = 0.03
r2 = 0.19
Residuals of Mean Length and Depth
Rugosity
Pygmy Rockfish
p = 0.99
r2 < 0.01
Residuals of Mean Length and Depth
Rugosity
Rosy Rockfish
p = 0.14
r2 = 0.10
Residuals of Mean Length and Depth
Rugosity
Squarespot Rockfish
p = 0.24
r2 = 0.06
Residuals of Mean Length and Depth
Rugosity
Starry Rockfish
p = 0.12
r2 = 0.11
Residuals of Mean Length and Depth
Rugosity



V
Blackeye Goby
Low (n = 153)
High (n = 156)
p = 1
Blue Rockfish
Low (n = 37)
High (n = 8)
p = 0.96
Painted Greenling
Low (n = 11)
High (n = 17)
p = 1
Pygmy Rockfish (Shallow < 55 m)
Low (n = 21)
High (n = 144)
p < 0.01
Pygmy Rockfish (Deep > 65 m)
Low (n = 478)
High (n = 449)
p < 0.01
Rosy Rockfish
Low (n = 72)
High (n = 51)
p = 1
Squarespot Rockfish
Low (n = 57)
High (n = 86)
p = 0.32
Starry Rockfish
Low (n = 10)
High (n = 8)
p = 1
Relative Frequency
Size Class (cm)

Appendix G Species group goodness-of-fit analyses with respect to three landscape-scale independent habitat variables. Results are reported for the proximity to edge (a), P:A ratio (b), and area (c)

a

	p	**x^2**	**df**
large rockfishes	0.955	0.003	1
dwarf rockfishes	0.671	0.181	1
large non-rockfishes	0.566	0.33	1
other benthic fishes	0.999	0	1

b

	p	**x^2**	**df**
large rockfishes	0.710	0.139	1
dwarf rockfishes	**0.012**	6.247	1
large non-rockfishes	0.592	0.396	1
other benthic fishes	0.626	0.237	1

c

	p	**x^2**	**df**
large rockfishes	0.062	3.481	1
dwarf rockfishes	**< 0.001**	12.914	1
large non-rockfishes	0.841	0.04	1
other benthic fishes	**0.011**	6.465	1

Appendix H Species observed in the edge zone, interior zone, or neither zone

Scientific Name	Common Name	Edge	Interior	Neither
Agonidae	Poacher	x		
Anarrhichthys ocellatus	Wolf Eel			x
Bathymasteridae	Ronquil	x	x	
Citharichthys sordidus	Sanddab	x		
Cottidae	Sculpin	x	x	
Damalichthys vacca	Pile Surfperch	x	x	
Embiotoca jacksoni	Black Surfperch	x	x	
Embiotoca lateralis	Striped Surfperch	x	x	
Hexagrammos decagrammus	Kelp Greenling	x	x	
Hydrolagus colliei	Ratfish	x	x	
Pleuronectiformes	Flatfishes	x		
NA	Unidentified	x	x	
Odontopyxis trispinosa	Pygmy Poacher	x		
Ophiodon elongatus	Lingcod	x	x	
Oxyjulis californica	Senorita			x
Oxylebius pictus	Painted Greenling	x	x	
Phanerodon spp.	Surfperch	x	x	
Phanerodon atripes	Sharpnose Seaperch	x	x	
Phanerodon furcatus	White Seaperch	x	x	
Pholidae	Gunnel	x	x	
Raja binoculata	Big Skate	x		
Rathbunella hypoplecta	Stripedfin Ronquil	x	x	
Rhacochilus toxotes	Rubberlip Surfperch	x	x	
Rhinogobiops nicholsii	Blackeye Goby	x	x	
Scorpaena guttata	Striped Scorpionfish	x		
Scorpaenichthys marmoratus	Cabezon			x
Sebastes atrovirens	Kelp Rockfish		x	
Sebastes carnatus	Gopher Rockfish	x	x	
Sebastes caurinus	Copper Rockfish	x	x	
Sebastes chlorostictus	Greenspot Rockfish	x	x	
Sebastes constellatus	Starry Rockfish	x	x	
Sebastes emphaeus	Puget Rockfish	x	x	
Sebastes ensifer	Swordspine Rockfish	x	x	
Sebastes entomelas	Widow Rockfish	x	x	
Sebastes flavidus	Yellowtail Rockfish	x	x	
Sebastes helvomaculatus	Rosethorn Rockfish	x	x	
Sebastes hopkinsi	Squarespot Rockfish	x	x	
Sebastes jordani	Shortbelly Rockfish		x	
Sebastes maliger	Quillback Rockfish	x	x	

Sebastes melanops	Black Rockfish	x		
Sebastes miniatus	Vermilion Rockfish	x	x	
Sebastes moseri	Whitespeckeled Rockfish			x
Sebastes mystinus	Blue Rockfish	x	x	
Sebastes nebulosus	China Rockfish	x	x	
Sebastes ovalis	Speckled Rockfish	x	x	
Sebastes paucispinis	Bocaccio	x	x	
Sebastes pinniger	Canary Rockfish	x	x	
Sebastes rosaceus	Rosy Rockfish	x	x	
Sebastes ruberrimus	Yelloweye Rockfish	x	x	
Sebastes rufus	Bank Rockfish	x	x	
Sebastes semicinctus	Halfbanded Rockfish	x	x	
Sebastes serranoides	Olive Rockfish	x	x	
Sebastes serriceps	Treefish	x	x	
Sebastes spp	Rockfish	x	x	
Sebastes wilsoni	Pygmy Rockfish	x	x	
Sebastes zacentrus	Sharpchin Rockfish	x	x	
Sebastolubus spp	Sebastomus	x	x	
Stichaeidae	Prickleback	x	x	
Torpedo Californica	Pacific Electric Ray		x	
Zalembius rosaceus	Pink Surfperch	x	x	
Zaniolepis frenata	Shortspine Combfish	x	x	